Models of Bontebok (*Damaliscus pygargus pygargus*, Pallas 1766) habitat preferences in the Bontebok National Park and sustainable stocking rates

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ABSTRACT

This study concentrates on the Bontebok (*Damaliscus pygargus pygargus* Pallas 1766) population of the Bontebok National Park. Using a combination of literature research, field observations, satellite imagery, Geographic Information System mapping and dung analysis, their habitat preferences within the Park are ascertained and compared to different behavioural and environmental factors. Considering vegetation composition and height, grass cover, burning history, general topography, water availability, actual diet quality (from faecal analysis) and population distribution, the best predictor of spatial pattern are investigated with GIS Dempster-Shafer models. The historical density distribution of the animals in the Park can be used to predict sustainable stocking rates. As far as possible, the results for the Bontebok are compared to those of the other larger herbivores in Bontebok National Park i.e. Red Hartebeest, Cape Mountain Zebra and Grey Rhebuck. These results should be useful for Wildlife Managers to know how to manage veld for Bontebok and at what stocking rates this can be done sustainably.

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OPSOMMING

Hierdie studie fokus op die Bontebok (*Damaliscus pygargus pygargus,* Pallas 1766) bevolking van die Bontebok Nasionale Park. Deur ‘n kombinasie van literatuurstudie, veldobservasies, satlietbeelde, Geografiese Inligtingstelsel (GIS) kartering en mis-analise te gebruik, word Bontebok habitatvoorkeure in die Park vasgestel en met verskillende gedrags- en omgewingsfaktore vergelyk. Deur te kyk na plantegroei-samestelling en hoogte, grasbedekking, brandgeskiedenis, algemene topografie, water-beskikbaarheid, diëet kwaliteit en die Bontebokke se waargenome ruimtelike verspreiding, word die faktor wat die verspreidingspatroon die beste voorspel, m.b.v. GIS Dempster-Shafer modelle ondersoek. Die historiese digtheidsverspreiding van diere in die Park word gebruik om volhoubare veldladings te voorspel. Sover moontlik word die resultate vir Bontebok vergelyk.met die ander groter herbivore in die Bontebok Nasionale Park, te wete Rooi Hartebees, Kaapse Bergsebra en Vaalribbok. Hierdie resultate behoort vir Natuurlewe-bestuurders tot nut te wees as riglyne vir veldbestuur en volhoubare veldladings van Bontebok.

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Chapter 1
Introduction to the carrying capacity concept for mammalian herbivores and habitat preferences of Bontebok (Damaliscus pygargus pygargus, Pallas 1766)

General Introduction

Wildlife managers are frequently confronted with managing numbers of animals. The carrying capacity concept is most widely used and frequently determined by simply adapting agricultural recommendations (e.g. Boshoff et al. 2001). In this study, I propose that adaptive management is a better approach (Grossman et al. 1999) because of practical and theoretical problems with the carrying capacity concept. As an alternative, I propose habitat preferences as one of the more useful tools available for adaptive wildlife management.

Although "carrying capacity" is used for plant populations and predators as well, here only herbivore populations will be considered. This is for a number of reasons:
1) The terminology of carrying capacity concepts developed mostly in grazing systems and there found most of its application.
2) Herbivores are a special case. The resources for plant populations are mostly (relatively stable) abiotic environmental factors (the limiting factors (Liebig 1840, quoted in Boughey 1968)) while predator populations can depend on two or more fluctuating prey populations that are usually perfectly substitutable (Begon et al. 1996).

Neither of these conditions is valid for most herbivore populations. Herbivores are seldom directly dependent on environmental factors, but rather are dependent on dynamic plant populations for their food and furthermore, the different plant species (and even different parts of plants) are not perfectly substitutable (Owen-Smith & Novellie 1981). Plant quality can be just as important as, or even more important than simply the quantity of available plant material (Hobbs & Swift 1985). In the Cape Floristic Region, it is mostly large mammalian herbivores that are considered for re-introduction. However, the ability of natural Renosterveld and especially Fynbos to sustain these herbivore populations is uncertain (Boshoff et al. 2001).

The Fynbos biome forms part of the Cape Floristic Kingdom and it is considered one of the biodiversity hotspots in the world (Myers et al. 2000). The area used to have numbers of large herbivores and predators (Skead 1980). Most of them have gone locally extinct; one species (*Hippotragus leucophaeus*) and one subspecies (*Equus quagga guagga*) went globally extinct. The only larger herbivore to survive in the Fynbos biome to the present ((Skead 1980, Van Rensburg 1975), is the Bontebok (*Damaliscus pygargus pygargus* Pallas 1766) previously known as *Damaliscus dorcas dorcas* (cf. Rookmaaker 1991, Wilson & Reeder 1993). Because the Bontebok National Park includes the largest patch of conserved coastal Renosterveld (Rebelo 1996), it was chosen as the study site for investigating these questions on carrying capacity, sustainable stocking rates, adaptive management and habitat preferences.

First, the "carrying capacity" concept is examined in the literature and some of its shortcomings demonstrated. Then, the use of habitat preferences in the management of large mammalian herbivores is considered. Finally, this approach is demonstrated by a study done on the Bontebok (*Damaliscus pygargus pygargus*, Pallas 1766) in the Bontebok National Park.

Search for the mythical carrying capacity

Introduction

"The maximum population size that can be supported indefinitely by a given environment, at which intra-specific competition has reduced the *per capita* net rate of increase to zero. An idealised concept not to be taken literally in practice" (Begon et al. 1996).

The "carrying capacity" concept has a long history in ecology ever since the proposal of the logistic equation by Verhulst (1838, cited by Begon et al 1996). All too often, it has been taken literally in practical veld management.

Like all mythical creatures, "carrying capacity" has been elusive (Dhondt 1988). Here I attempt to track it down as the concept has developed since the term was first used by Hadwen & Palmer in 1922 (cited in Seidl & Tisdell 1999), defined roughly by Leopold in 1933 (1961) and reincarnated into a pantheon of different avatars (Dhondt 1988, Bartels et al.

1993). Methods used by others in their attempts to find a "carrying capacity" are examined to show just how elusive a "carrying capacity" can be. The main reason for this elusiveness is then shown when the spotlight falls on the theoretical underpinnings and hidden assumptions of the carrying capacity concept. Finally, we leave the area of mythology and speculation to consider the alternative, more realistic approach.

Terminology

Dhondt (1988) already complained about the confusing nature of the term "carrying capacity" (see also Bartels et al. 1993). To find it, we first of all need to know what it is. Since Odum (1953, quoted in Dhondt 1988), it has frequently been considered as equivalent to K used in the logistic and the Lotka-Volterra equations (Begon et al. 1996, Mentis 1977, Hobbs & Hanley 1990, Lindenmayer & Lacy 2002). The logistic equation [$dN/dt = rN((K-N)/K))$] simply states that populations show a sigmoidal growth curve approaching a stable "equilibrium density" (= K) (Begon et al. 1996) (Figure 1). However, since carrying capacity, defined as the ability of a certain area to sustain a population indefinitely, is a property of the environment, while K is a property of a population, they can strictly speaking not be equivalent. Here the term "equilibrium density" will be used for K (Dhondt 1988).

In 1970 Sharkey refined the carrying capacity concept by noting that the biomass of populations are likely more important than simply the numbers of animals. Mentis (1977) concluded that biomass itself was inaccurate and that the energy requirements of animals should be used instead.

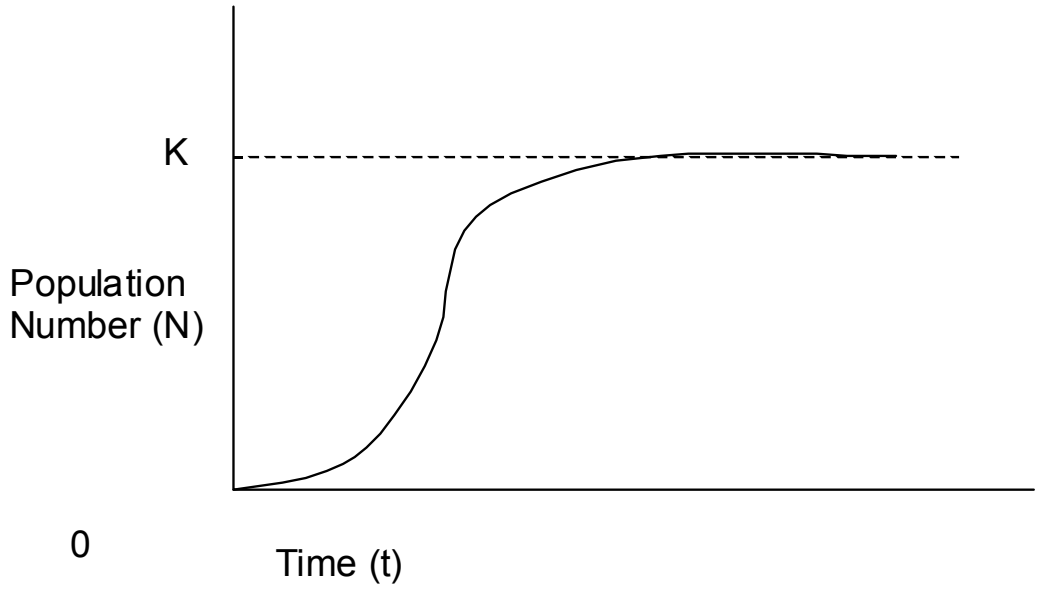

Figure 1 The logistic curve. K assumed constant with exponential and density-dependent growth leading to equilibrium at K ($dN/dt = rN((K-N)/K)$ where N = population size, r = intrinsic growth rate and K = equilibrium density).

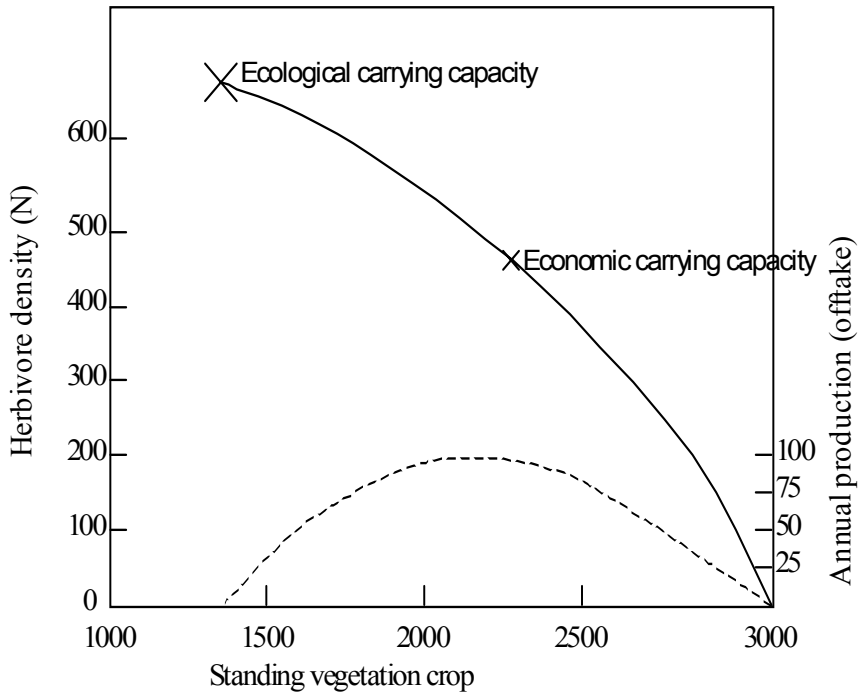

Figure 2 The isocline of equilibrium (possible values for K) between plant density and herbivore density (shown by solid line), with the rate of harvesting (or predation) (dotted line) needed to impose the equilibrium, and the sustained-yield annual off-take (useful production) that can accrue from the herbivore population. Veld managers aiming for production would need the vegetation status to be maintained at the level where maximum off-take is possible (economic carrying capacity, cf. Jones & Sandland 1974), while managing for a natural system (without predation, though) would result in equilibrium where there is no net growth in the animal population (K) because of the decrease in vegetation status (ecological carrying capacity) (From Caughley 1976).

Caughley (1976) clarified the concept a bit by recognising that "ecological carrying capacity" and "economic carrying capacity" were two separate versions of the idea. He saw carrying capacity as "the concept of vegetation-ungulate equilibrium" resulting in a continuous line of possible values (for K) (Figure 2). Different people have called two points on this curve "carrying capacity". The one is the point where the nutritional value available per individual animal has fallen to the level where the birth rate in the population equals the rate of mortality (either through higher mortality, or through lower birth rate or through both) and there is no net growth. The vegetation also stabilises permanently at this new (lower) productivity level. This is the way wildlife managers would normally use the term "carrying capacity", and was termed "ecological carrying capacity" by Caughley (1976). Because no net growth occurs at this point, there is no excess of animals to harvest. It is therefore not a useful concept for range managers trying to optimise production. "The density of stock at equilibrium with the range conditions providing maximum sustained off-take is described as the carrying capacity or grazing capacity of the land" (Caughley 1976). This concept of carrying capacity Caughley (1976) termed the "economic carrying capacity".

Predation could cause a similar equilibrium density of herbivores that is lower than the ecological carrying capacity. This density was also called "carrying capacity" by Errington (1934, cited in Dhondt 1988). This reflects the case where the limiting factor (Liebig 1840, cited in Boughey 1968) for the herbivore population was cover from predation rather than nutritional requirements. Another, less confusing term used for this density by Errington (1934, quoted in Dhondt 1988) was the "threshold of security", the population density above which "superfluous" numbers of herbivores are particularly vulnerable to predation. The economic carrying capacity can be considered as a special case where the effect of harvesting by humans is the same as that of predation (the difference being that humans are much more efficient and can choose the level of "predation", so that there is no threshold of security).

"When the maximum wild density of grown individuals attained by a species, even in the most favourable local environments, tends to be uniform over a wide area, that maximum may be called the saturation point of that species" (Leopold 1961). This saturation point most likely reflects the effect of social structure, interference competition or territoriality in determining the maximum natural density of a species. Although not mentioned by name, this

concept has been used by Boshoff et al. (2001) to determine some of their spatial requirement estimates.

Grazing capacity can be considered as a special case of the carrying capacity concept, restricted to grazing herbivores. Heady (1975) said that grazing capacity is "the number of animals that produces the greatest return without damage to the physical resources and in concert with other values from the land." According to Caughley (1976), this is simply the equivalent of the economic carrying capacity (for grazers). Because wildlife management include more than one species, there has been some appreciation for the fact that the same environment provides different levels of nutrition for different species. Peel et al. (1998) criticize the use of the term "grazing capacity" for not taking into account the different forage sources and suggest the use of two terms, "grazing capacity" and "browsing capacity" with total carrying capacity as the sum of their values.

Although we distinguish between them, it is obvious that the equilibrium density (K) of a population will in many cases be determined primarily by the environmental carrying capacity. K reflects the density around which a population stabilizes as mortality and growth tends to become equal for whatever reason. If a grazing system is considered (Figure 2), this can be on any point along a continuum until the vegetation quality or quantity of the environment in which the population lives becomes the limiting factor at the ecological carrying capacity. Depending on the reason why equilibrium is reached before this point, these different K-values can then be considered as different types of carrying capacity. There are almost as many possible values for K as there are animals in a population. However, for a certain environment there should be only one ecological carrying capacity, one economic carrying capacity (normally about 1/2 K (Begon et al. 1996)), if shelter from predators are limiting, only one threshold of security, if interference competition becomes the limiting factor, only one saturation density, etc. Each of these "carrying capacities" could be considered the result of a different management objective.

In addition, to the above, there are a number of other definitions of "carrying capacity and related terms that evolved from it (see Dhondt 1988, Bartels et al. 1993 for more). Stocking density is simply the number of animals (or biomass of animals) per unit area (Peel et al.

1998). Stocking rate is the stocking density per unit time (usually per year) (Peel et al. 1998). Here sustainable stocking rates are defined as the animal densities per unit time that can be sustained indefinitely without causing any long-term trends in the vegetation. The plural is used on purpose to show that there is possibly more than one value where herbivory won't change vegetation structure or quantity over the long term. It also takes into account that the actual stocking density necessary to be sustainable might change from year to year and differ for different populations and different species. This is the sustainability equivalent of what is called “stocking intensity” in Trollope et al. (1999). If equilibrium conditions are assumed, a single sustainable stocking density with no time dimension could theoretically also be proposed.

Because more than one stocking rate is possibly sustainable, the best stocking rate to be used in a certain situation will depend on the specific management aims. Wildlife conservation managers usually aim for the greatest possible biodiversity in a certain area that is sustainable. It is unlikely that this goal will be satisfied at ecological carrying capacity. This implies that there can be added at least one more kind of carrying capacity; I shall call this the biodiversity capacity and it can be considered as that equilibrium density of animals where the total biodiversity in the ecosystem is at its greatest and where the herbivory doesn't cause long-term changes in the vegetation.

Connected to the idea of both sustainable stocking rates and the different definitions of carrying capacity, are the terms ‘overstocking’, ‘overuse’ and ‘overgrazing’. Heady (1975) distinguish them on the grounds that stocking is a daily phenomenon, forage use is seasonal and grazing has a longer time scale. He defines overstocking as something that can be corrected in a day; overuse (overutilization) can be corrected in one growing season, while the effects of overgrazing may take several years to reverse. I would add the term “degradation” (cf. “dryland degradation” in Dean et al. 1995) that includes, in addition to the direct effect on vegetation, the effect on physical resources and may not be reversible at all in human time scales.

Now that we have the "true" definitions of carrying capacities, we should be able to at least recognise it, and can now consider the methods used by others in their search for this mythical beast.

Methods used to ascertain carrying capacity

As we saw above, "carrying capacity" exists in more than one form. Unfortunately, it is seldom clearly stated in the literature *which* carrying capacity is being determined. It is this confusion that led Dhondt (1988) to suggest that the term should rather not be used at all (see also Bartels et al. 1993).

Since the carrying capacity concept in general assumes that equilibrium is reached between the herbivore population and the vegetation community, three different approaches to find the carrying capacity is possible:

1) Consider the animals at their equilibrium density (Jones & Sandland 1974, Fynn & O'Connor 2000, Brooks et al. 1977, Sharkey 1970, Bell 1982, East 1984, Van Gils 2004, Kotler et al. 1994, Steenekamp & Bosch 1995).

2) Consider the vegetation and find the herbivore density at which no detrimental change in vegetation occurs (Caughey 1976, Vorster 1999, Du Toit 2000, Hardy et al. 1999, Tainton 1999, De Leeuw & Tothill 1993).

3) Combine the two methods by looking at both plants and animals (Caughley 1976, McLeod 1997, Mentis 1977, Hobbs & Swift 1985, Novellie 1987, Owen-Smith 1994, Muya & Oguge 2000, McAllister 1967, Barker 1986, MacLeod et al. 1996, Erasmus et al. 1978, Grant et al. 1995, 2001, Wrench et al. 1997, Stuth et al. 1999, Li et al. 2000).

Peel et al. (1999) recommend that a variety of methods be used, first at coarser scale for a region and then at a finer scale for a specific ranch/farm. Included at regional scale would be rainfall, geology, soil types, vegetation types, use of existing medium-term range assessment data, nutritional status of game related to rainfall, soil, stocking density and vegetation condition, using thresholds of potential concern (Grant et al.2001), together with the management objectives. At the more local level, long- and short-term rainfall data and distribution, geology, soil types, vegetation types, NDVI (normalised difference vegetation index) used as index of active growth, a moving standard deviation index, local short- and medium-term range assessment data compared to regional data, nutritional status of game

relative to rainfall, soil, stocking density and vegetation condition, identification of key resource areas, thresholds of potential concern, together with the management aims are used to set the appropriate stocking density and species mix. However, they recommend that more research is needed on integrating these methods, especially with regard to the different equilibrium and non-equilibrium paradigms that lie at the basis of determining "stocking rate", "carrying capacity" and related indices.

Just how elusive "carrying capacity" can be, was shown by one of the few studies to actually compare different methods of determining "carrying capacity" (Schmidt et al. 1995). They compared a method making use of both veld condition and rainfall (Danckwerts 1989) to one using only rainfall (cf. East 1984) and to one using herbaceous phytomass (Moore & Odendaal 1987, quoted in Schmidt et al. 1995). It should be noted that the method using phytomass gave a short-term (one year) "carrying capacity" only and is therefore not really a method for determining carrying capacity as defined above. In general they found that the method using rainfall only gave the most conservative numbers, followed by the short-term phytomass method, with the method combining veld condition and rainfall giving the highest estimate of carrying capacity. All three of these methods gave a number that was less than the long-term agricultural grazer stocking rate. Methods using rainfall are able to give in addition to the long-term estimate based on average rainfall, a short-term estimate based on the rainfall in a specific year. The short-term estimates of all three methods were ≤ 50% of the long-term agricultural grazer stocking rate recommendation.

The inadequacies of veld management based on carrying capacity are shown by the fact that, e.g. in the Karoo there has been an ongoing decrease in stocking rate since 1855; today it is almost half the rate of 100 years ago (Dean et al. 1995). This effect might also include the alleged spread of Karoo vegetation into grassland and savanna areas. Similar evidence of veld degradation is seen in other parts of Africa despite consistent efforts by range scientists to prevent it, usually using the carrying capacity concept as the basis for management (Behnke & Scoones 1993, Oba et al. 2000).

Ecological and economic carrying capacities actually try to measure two different things. Although economic carrying capacity can generally be estimated as being half the ecological

carrying capacity, this is not always the case. The same methods might not be equally useful for both. In addition, different theoretical assumptions lie at the heart of the different methods (Peel et al. 1999). It is seldom clear as to which method is the most useful in a certain situation. Unless management aims are explicitly stated, the calculated "carrying capacity" might be totally inappropriate for the specific situation. In addition, no methods could be found in the literature describing at which stocking rates maximum biodiversity can be expected. To make things even more complicated, there might be more than one management aim (e.g. high numbers of visible herbivores for tourist viewing / hunting, but also maintenance of plant biodiversity).

Peel et al. (1999) made clear the importance of scale and of herbivore species in determining carrying capacities. At coarser spatial scales, even though individual patches may change over time, the relative abundance and size of patches in different states may remain relatively constant (equilibrating landscapes). At finer scales, e.g. most fenced farms and camps, fewer patches will be included and temporal changes should seem more pronounced (non-equilibrating landscapes). Larger areas also allow migration, which might compensate for the effects of spatial variability. Mentis (1977) focused on the different herbivore species, their requirements in terms of graze and/or browse, their ability to switch between these two food sources and their relative selectivity. All of these factors are even more important in multi-species systems, especially their effect on resource partitioning of the available food, competition and facilitation. None of these factors are adequately taken into account in any of the current methods used for determining carrying capacity.

Peel et al. (1999) mention that the effect of the whole debate on equilibrium vs. non-equilibrium grazing system models has been to make it unclear as to what model is applicable in a certain environment. I propose that there is in reality a continuum of systems, from those with greater variation in rainfall (mostly arid and semi-arid areas) and a larger influence of abiotic factors to those with less variability and greater biotic interaction effects in temperate, high-rainfall areas. In between, there might be any combination of biotic and abiotic influences (cf. Fynn & O'Connor 2000). In addition, there is the whole issue of bottom-up vs. top-down control of grazing ecosystems (Begon et al. 1996).

Possibly the largest practical problem in determining carrying capacity (and sustainable stocking rates) is the question of how to ensure sustainability. Even when long-term data are used, there is very little guarantee that any method used to determine "carrying capacity" would give a sustainable stocking rate. The effects of droughts, fire and other stochastic environmental fluctuations make it even more difficult to be sure that a specific carrying capacity is actually sustainable. A general guideline in this regard can be to say that if complementary feed is necessary to fatten animals for the market, they can be considered to be already above the current economic carrying capacity, whereas if feed is needed to keep a certain population alive, the current ecological carrying has been exceeded. These situations frequently arise even when animals are at densities lower than the official "carrying capacity". However, such guidelines may not be practical; it is also possible in some cases that the complementary feed merely accelerates the production rate above that of the economic "carrying capacity", but without actual deterioration in veld condition. Although we investigated a number of methods used for determining carrying capacity, there still exists no way of ensuring that the resultant stocking density is actually sustainable in the long run. After all these years, the mythical "carrying capacity" has remained elusive.

Why is it so difficult to determine carrying capacity?

When we take a closer look at the roots of the carrying capacity concept, a number of implicit (very seldomly stated) assumptions come to light:

1. Carrying Capacity is a unique measurable property of the environment
2. Carrying Capacity is relatively constant (i.e. little or no environmental impact on CC)
3. Carrying Capacity is mostly/exclusively determined by food availability (plant-herbivore interaction)
4. Herbivores have little/no effect on the Carrying Capacity.

We already saw that carrying capacity is not unique. There exist at least two "carrying capacities" viz. economic and ecological carrying capacity. They have in common that one fixed figure is given to describe the herbivore density of either maximum production or maximum population size for a certain area. Depending on the management aims, even more "carrying capacities" are possible, e.g. a biodiversity capacity. Any determination of carrying capacity that doesn't make explicit what is being measured, is defective. If carrying capacity

was truly a unique and measurable property of environments, it should be expected that the different methods used to determine it, should give similar answers. As can be seen from attempts at this (e.g. Schmidt et al. 1995), it is seldom the case. This would suggest either that the methods used to determine carrying capacity are defective (and it would be impossible to know which ones are reliable) or that no unique carrying capacity actually exists. One reason for the differences in carrying capacity estimates is that different ecological models are assumed (McLeod 1997).

Recently, the assumption of equilibria between herbivores and their supporting plant communities has been questioned (Ellis & Swift 1988, Behnke et al. 1993, Oba et al. 2000). They proposed that, especially in arid and semi-arid regions of Africa, environmental stochasticity (mostly in rainfall) would prevent ecosystems from reaching equilibrium. Droughts will decrease herbivore numbers before they reach high enough densities to have an impact on the vegetation. Here, the implicit assumption is that under these conditions, bottom-up processes will control the ecosystem rather than top-down processes. The idea of one, unique Clementian climax (=vegetation in "good condition") has also been challenged (Westoby et al. 1989) and an alternative state-and-transition model proposed. The weakness of this model lies in the fact that it is *post hoc*: it doesn't give a mechanistic explanation for transitions and therefore cannot predict changes unless they have been observed to occur elsewhere. In addition, both of these methods can be faulted for inadequately considering edaphic factors and topography. By having an average "carrying capacity" the fact that slopes and certain soil types are more likely to degrade (and thus have a lower carrying capacity) than flat, fertile areas are not taken into account (Fynn & O'Connor 2000). The effect might be that slopes become degraded while the stocking density is still below the "carrying capacity". Alternatively, not enough is made of the selectivity of different species of herbivores; they might avoid areas of higher degradation risk and instead "overgraze" the more resilient patches without any real degradation happening, even at numbers higher than the "carrying capacity". Carrying capacity changes because of rainfall or fire, adds more uncertainty to the concept.

All the carrying capacity models considered in the literature assumed that carrying capacity are determined by food availability. However, the greater availability of water points is

frequently mentioned (Behnke & Scoones 1993, Dean et al. 1995, Peel et al. 1999) as a cause of veld degradation, especially through piosphere effects (Tainton 1999, Brits et al. 2000). One explanation for the degradation caused by piospheres, is that around natural water points (fountains, streams, etc.) a higher ground water table can be expected, causing the growth of vegetation that is more resilient to grazing/browsing pressure. Instead, artificial water points are many times in areas where ground water is deep and the vegetation not adapted to grazing in all seasons. Water-dependent herbivores may now occur in vegetation types where they would not normally be found, except maybe in the rainy season (if the soil allows surface water to form temporary pools). Once again, rainy season pools are most likely to occur in low-lying areas where less erosion and richer soils can be expected (Fynn & O'Connor 2000). For many species, (seasonal) stocking rates are determined by drinking water availability and not, as is commonly assumed, by food.

The possibility that predation has always kept herbivore densities far below the "ecological" carrying capacity, is also seldom considered. In this scenario, surface water might again play an important role. In drought years, less surface water should be available, meaning that water-dependent herbivores will have to use the decreasing number of available water points. This should make it easier for predators to catch them by just waiting close to water points instead of having to search over wider areas. The effect might even be of changing a system that was controlled by bottom-up processes (forage availability) to one controlled by top-down processes (predation).

The fact that carrying capacity is usually given as a single density that does not change over time would seem to indicate bottom-up control of herbivore numbers. Most models (the model by Caughley 1976 is the one major exception) assume implicitly that herbivores have little or no impact on the carrying capacity, which stays constant. However, the very idea that management of herbivore numbers is necessary or advantageous to prevent overgrazing or degradation, implies that some top-down effects also play a role and forces one to conclude that, at least in some situations, herbivores might have a larger impact on vegetation than vice versa. The assumption remains that maximum production/off-take would normally occur at a fixed equilibrium density, called the (economic) carrying capacity. Some models assume that

overgrazing will not change the carrying capacity permanently, but can be rectified by lowering herbivore numbers. This assumption is probably not true in some situations.

Thus, the assumption of a single, stable carrying capacity can be seen to break down in many situations. When we consider the theoretical underpinnings of the ecological carrying capacity in particular, the defects of this concept are seen more clearly. Figure 1 shows the logistic curve as seen in many ecology text books (cf. Begon et al. 1996). Caughley (1976) has already criticised the logistic equation for not using parameters with biological meaning. Although the equilibrium density can be determined by different factors, it is a basic assumption of many carrying capacity models that food availability and competition for food are the main causes of equilibrium being reached and therefore that K = carrying capacity. It has been recognized that population numbers in nature seldom reach a totally stable equilibrium. Instead, an overshoot of K followed by damped oscillations around K has been proposed as a more realistic version of the logistic equation by including time lags (Caughley 1976, Begon et al. 1996) (cf. Figure 3). K is still assumed to be constant (the assumption of herbivores having little effect on vegetation). Sometimes (depending on the parameter values in the logistic equation) stable limit cycles (as shown in Figure 4) can be produced by the modified logistic equation. Other parameter values can give rise to chaotic, unpredictable population behaviour as shown in Fig.7. In both cases, K is still assumed to be constant (Begon et al. 1996).

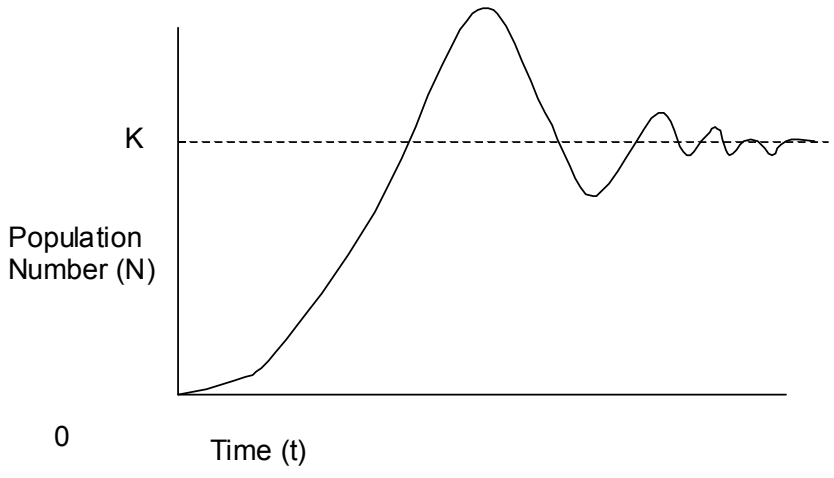

Figure 3 *Overshoot. Because of e.g. long generation time, population doesn't react to density dependent factors before overshooting K. Damped oscillations lead to equilibrium around K. Constant K still assumed.*

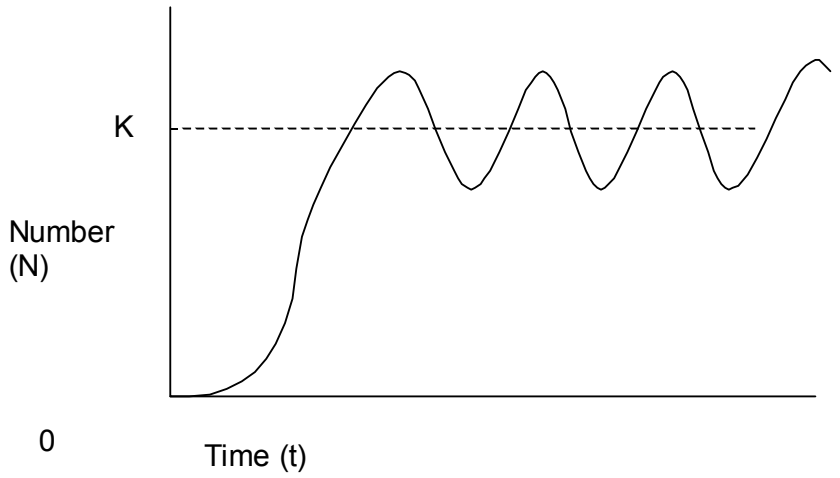

Figure 4 *Stable cycles. Population overshoots with no damping and results in stable oscillations around K. K still assumed constant.*

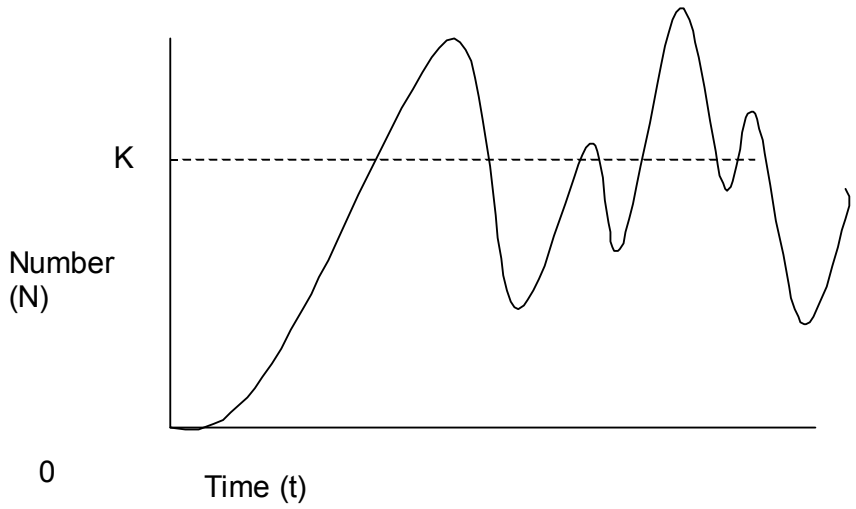

Figure 5 *Chaos. K still assumed constant. Because of lag, relative long generation time and/or rapid growth, population changes unpredictably around K with repeated overshoots and crashes, but still within certain limits.*

In contrast to the models above that assumed a constant equilibrium density (and carrying capacity if we assume carrying capacity = K), a seasonally varying K (Figure 5) or stochastic variability in K (Figure 6), can be proposed. The last case would be similar to the situation as described by Behnke et al. (1993) for arid and semi-arid rangelands in Africa with K dependent on the varying rainfall. They went as far as proposing that herbivore numbers become decoupled from the plant community structure, instead depending only on the amount of rainfall. Their assumption that droughts will cause a decrease in herbivore numbers before they ever reach numbers high enough to have a permanent effect on the vegetation is shown by Fynn & O'Connor (2000) as not applicable for cattle in semi-arid lowveld savanna vegetation. However, their method was more applicable to the situation on commercial farms and included the feeding of animals in dry years to keep their numbers artificially high. Although they concluded that the non-equilibrium paradigm is not applicable to that specific area, it is still possible that a non-equilibrium system was indeed at work, but without the decoupling between vegetation and herbivore numbers hypothesized by Behnke et al. (1993).

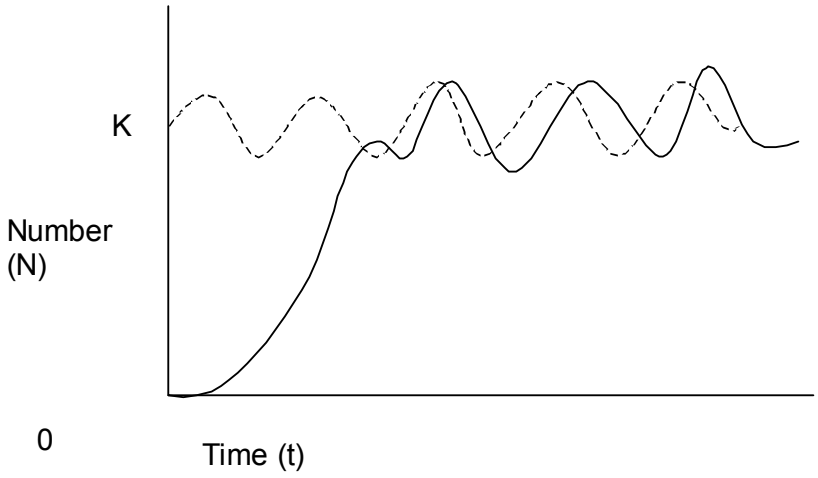

Figure 5 *Seasonally varying K. Population grows exponentially, but density dependent, follows K as it cycles seasonally. No single equilibrium is possible.*

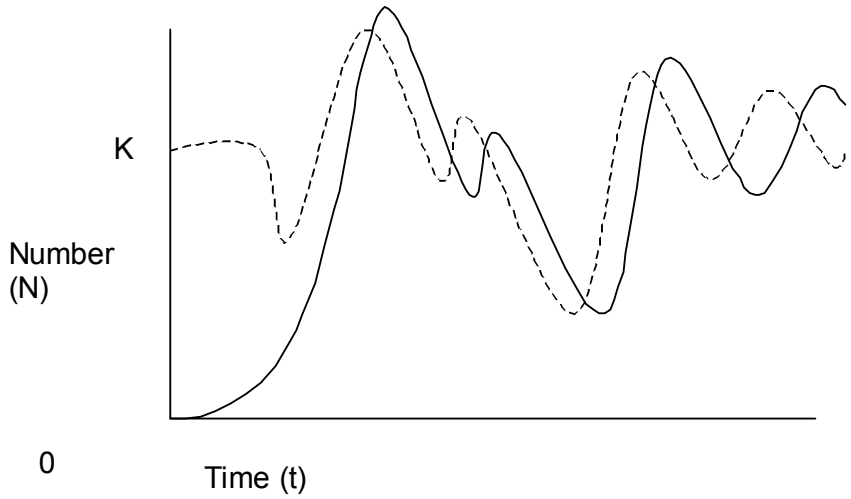

Figure 6 *Stochastic variation. K varies unpredictably (and independently from N). Density dependent population growth results in population mimicking unpredictable K.*

In addition to the possible non-equilibrium situation as proposed by Ellis & Swift (1988), Behnke et al. (1993) and others, it is also probable that herbivores indeed have a much larger effect on the carrying capacity than what is usually assumed. Indeed, it might be the case that whenever there is an overshoot (eruption) situation, the carrying capacity is lowered, resulting in degradation. This scenario is shown for an environmentally-stable situation in Figure 7 and for a non-equilibrium situation in Figure 8. That these possibilities are not adequately considered is possibly the greatest theoretical shortcoming in the current carrying capacity concept. It is probable that these decreases in carrying capacity would occur mostly in small steps and are therefore not noticed immediately, but only after longer time periods.

The situations of "overshoot" causing a decline in carrying capacity as proposed here, are applicable to the idea of K as an approximation of ecological carrying capacity. However, it is possible, especially in a variable environment, that sometimes the mean "economic carrying capacity" is still higher than the "true ecological carrying capacity" at that point in time. In this case, overgrazing and/or degradation might still occur. This situation is much

less likely in a more stable ecosystem. That this whole process is most likely slow and possibly irreversible, is confirmed by some case studies (e.g. Dean et al. 1995).

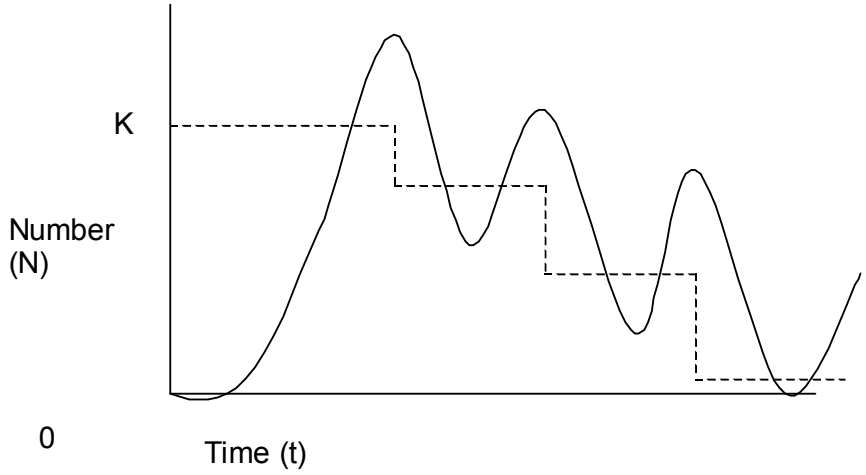

Figure 7 *Degradation/overgrazing. Overshoot of K causes decline in K. Very low K resulting. (The same effect can be had on a stable cycling N, seasonal cycling and even stochastic K). In the last two cases the Maximum and minimum values of K (and N) would tend to decrease. As long as K remains relatively constant, it cannot be called overgrazing. Note that in this model overgrazing cannot occur if density-dependence prevents N from exceeding K.*

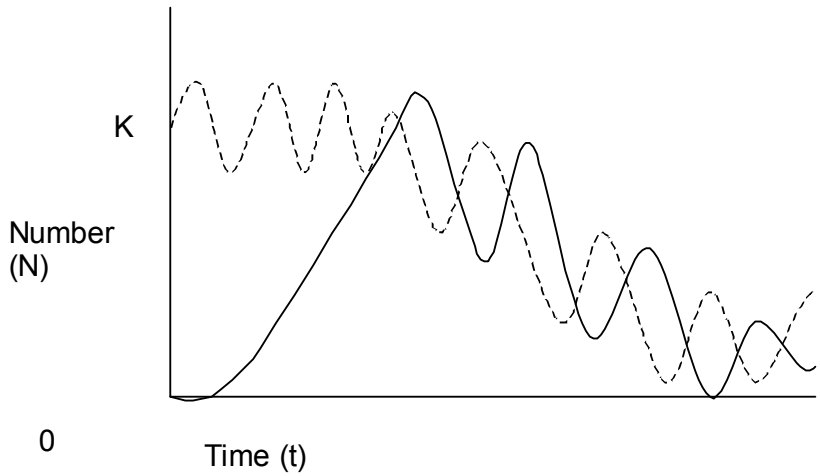

Figure 8 *Even with cycling K overgrazing can still occur and have a similar effect as with "constant" K. With stochastic variation in K, overshoot might be even more likely, leading to a similar decline in carrying capacity.*

Conclusions: back to reality

There are many problems connected to the carrying capacity concept, both practical and theoretical. Much more than simply being a matter of unclear terminology as shown by Dhondt (1988), the very concept of carrying capacity is based on unsound assumptions and might lead to overgrazing or land degradation when insufficient consideration is given to environmental stochasticity. On the one hand, it is possible that many cases of "overgrazing" indeed simply represent an equilibrium point where the vegetation community has a low biomass and the herbivore population densities are relatively high. Because some compensatory growth is possible (cf. McNaughton 1984), it is possible that even though less palatable and less nutritious, these plant communities might still produce more forage than a plant community with higher biomass and/or species richness. The management aims would determine if such a situation is considered advantageous or not. In contrast, there are numerous examples of situations where overgrazing/degradation might occur while herbivore densities are well within the limits of the carrying capacity.

It is not claimed here that there exists no limit to herbivore population size. The proposal is rather that a single "carrying capacity" is a useless measure of this limit in most cases, and might actually cause degradation if used indiscriminately. In particular, it is proposed that sustainable stocking rates should be seen not as a single value, but as a changing property than cannot be known for sure. Therefore, the concept of the single carrying capacity like any myth, has its origin in some reality, but does not describe reality *in toto*. It is proposed that, if carrying capacities are used, some indication of the possible variability in the carrying capacity should be included and that an estimate of both ecological and economic carrying capacity should be given. The need for this has been seen e.g. in a study by Danckwerts (1989) who showed that the actual grazing capacity was within 25% of the long-term mean grazing capacity for only two years out of every ten. Instead of the mythical carrying capacity, an approach of adaptive management is advocated (Grossman et al. 1999, Tainton 1999). Factors such as the timing of grazing, water and piosphere effects, the herbivore

species and the specific habitats that are being grazed (e.g. vegetation type, soil type, and topography of the area) may be more important than stocking rates for ensuring sustainability. In arid and semi-arid regions in particular, rainfall may be more important than any other factor. In general, it can be stated as a rule of thumb that the less rainfall an area receives and the more variability in extreme environmental factors (such as rainfall and temperature) there is, the less useful the idea of carrying capacity becomes. However, even in more stable systems where equilibrium assumptions are more likely to be true and there is less need to regularly adjust stocking rates, the fact that different methods give different results, should caution managers about the reliability of "carrying capacity" estimates. The interaction between the different herbivores and the plant communities in which they occur, should be monitored and herbivores managed according to the management aims. In particular, the habitat preferences of different herbivore species and the reasons for these preferences might be a better management tool to find limitations in herbivore densities than the carrying capacity concept.

The use of habitat preferences in the management of large mammalian herbivores

Terminology

As far back as 1973, Whittaker et al. complained that two of the most important terms in ecology, "niche" and "habitat", are among the most confused in usage. By 1997, Hall et al. again pleaded for standard terminology in using the habitat concept. The simplest definition of habitat is simply the "place where a microorganism, plant, or animal lives" (Begon et al.

1996). Hall et al. (1997) defined "habitat" as "the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism". "Wherever an organism is provided with resources that allow it to survive, that is habitat" (Hall et al. 1997). This is similar to the simpler definition, but gives a more important place to the different resources (including space). In this sense, it is closer to the definition of Whittaker et al. (1973) who saw "habitat" as a special case of the general multi-dimensional "niche" concept. Habitat is "the range of environments or communities over which a species occurs; the habitat hypervolume is an abstract formulation of this range…". They made a distinction between "habitat" and "niche" on the grounds that habitat has more of a spatial environmental component, measuring chemical and physical factors that would allow an organism to live in it, whereas "niche" is more concerned with the position of an organism within a certain community and the effects of biotic factors (Whittaker et al. 1973). This "niche dimensionality refers not to the number of biologically relevant factors in the environment, which may be virtually unlimited, but to the number of factors which serve to separate species" (Levins 1968 quoted in Ferrar & Walker 1974). Whittaker et al. (1973) proposed the term "ecotope" for the hyperspace of physical, chemical as well as biological factors that define where a species occurs (= habitat + niche). This term has not been used much afterwards, with "habitat" frequently being used both for "habitat" as defined above and for the "habitat + niche" concept. Similar to habitat, the term "biotope" was proposed to define the areas where a certain community (instead of a population) occurs. They considered that the term "habitat" might be used for a certain vegetation community in which an animal species is commonly found, because the range of the vegetation community (its biotope) is confined within certain environmental (chemical and physical) factors (Whittaker et al. 1973). In this case, the plant community acts as a proxy for the environmental factors that actually determine the distribution of the animal species. They also mentioned that it is not always easy to separate intercommunity (habitat) variables from intracommunity (niche) variables. In contrast, Hall et al. (1997) felt that "habitat type" as a term describing the type of vegetation association in an area or the potential of the vegetation to reach a certain climax stage, should be avoided when discussing wildlife-habitat relationships. Instead, they proposed that only the term vegetation association be used. Because a vegetation type might reflect physical or chemical environmental (habitat) factors that were not directly measured (Whittaker et al. 1973), as well as the fact that the term "vegetation association" might imply

that a full vegetation classification has been done (which is not always the case in habitat studies), I feel that "habitat type" might still be useful in some cases. One vegetation association area might also be heterogeneous in terms of physical factors such as topography. In these cases, it might be useful to distinguish these parts of the same vegetation association as different "habitat types". In this case, the understanding should be that it is not the biological "niche" of the organism within the community that is being considered, but the physical and chemical environment, partly provided by the vegetation. Because of the danger of confusion, the term "vegetation association" would still be preferred whenever a full vegetation survey and classification have been done. A number of other habitat-related terms were defined by Hall et al. (1997). "Habitat use" is the way an animal uses a collection of physical and biological components (resources) in a habitat. "Habitat selection" is a "hierarchical *process* involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment". "Habitat preference" is simply the outcome of this habitat selection process, resulting in disproportional use of some resources over others. "Habitat availability" is "the accessibility and procurability of physical and biological components of a habitat by animals", whereas "abundance" refers only to the quantity of a certain resource in the habitat. In general, abundance is much easier to determine than availability. "Habitat quality refers to the ability of the environment to provide conditions appropriate for individual and population persistence" and is a continuous variable. It might be that habitat quality will be different for survival, reproduction and population persistence because of the relative importance of the available resources. Other terms such as "suitable habitat", "nonhabitat", "unused habitat", "microhabitat", "macrohabitat" and "critical habitat" were also defined or rejected by Hall et al. (1997), but will not be considered here because of problematic usages.

Some theoretical aspects of habitat preferences

Bailey et al. (1996) emphasized the fact that habitat selection is a hierarchical process at different spatial scales from large scale (home range) decisions to small scale (bite) decision levels. Different factors are at work at different scales. Jarman & Sinclair (1979) mentioned that food, water, minerals, shade and cover to hide are all provided by vegetation. On the

negative side, vegetation also provides cover for predators, obstructs visual communications and consists of much inedible material in which herbivores must search for food. They considered food to be the most important of these factors. Considering vegetation, they mention that selection can occur at 3 different levels (a subset of the scales used by Bailey et al. 1996). Similar to the hierarchical model of Bailey et al. (1996), this selection can follow sequentially: first the vegetation community within which to feed, then the plant types or species to eat and lastly what parts of plants to eat. What they also showed was that not all species have the same emphasis on each level of selection and this might even differ between individuals of the same species (Jarman & Sinclair 1979). For some generalist species (bulk and roughage feeders) it might be enough to select a vegetation community without further regard to plant species or part, whereas more selective species would need to go through all these levels of decision-making at different time scales. However, at the vegetation community level, this selection is not always connected to food. In determining habitat preference, we can't always clarify the scale of selection. This might be because, in addition to larger scale (landscape) and longer temporal scale decisions determining where fine-scale selection occurs, fine-scale factors might again influence large-scale preferences (Bailey et al. 1996). Using three spatial scales, Melton (1987) demonstrated that herbivore species show a variety of seasonal patterns at different scales, suggesting that different optimising strategies are used at different scales.

One major aim of habitat studies is to clarify the interspecific competition and/or facilitation effects (Melton 1987, Vesey-FitzGerald 1960, Perrin & Brereton-Stiles 1999). Where competition for food is the most important factor determining habitat preferences, habitat selection can be seen as a branch of optimal foraging theory (Melton 1987, Rosenzweig 1985). Where these include inter-specific competition effects, it is actually niche (the position of a population within the community) rather than habitat that is being measured (Whittaker et al. 1973). Virgós (2001) showed that in heterogeneous landscapes, habitat quality was more important when there was little habitat fragmentation, whereas isolation (distance to next habitat patch) was most important in fragmented habitats for determining badger sett densities. A similar pattern can be postulated for other species. This indicates that, in fragmented habitats, dispersal theories (like the island-biogeography model, MacArthur & Wilson 1963) could be more important than either competition (niche position) or habitat

quality. The quality of the matrix within which the high-quality habitats are found would probably determine if this model is applicable because island-biogeography models generally assume the matrix to have no value at all for dispersing organisms (MacArthur & Wilson 1963).

Methods used to determine habitat preferences

There are basically two types of methods that can be used to determine habitat preferences. The first group of methods uses some experimental perturbations of the system to infer the factors of habitat preference. The second group of methods observes the animals in their natural habitat and uses their density distribution (or absence/presence) to infer which habitats they prefer. Habitat can be determined either before the observation of animals (e.g. Dörgelog 1998) or (smaller scale) only where animals were observed (Dekker et al.1996). This last method has the disadvantage of not measuring habitat variables where no animal observations were recorded. However, because these measurements of habitat are usually at different scales the two methods are often combined (e.g. Dekker et al. 1996). The habitat types can be determined in a number of ways. These include using the results from previous studies (e.g. Winkler & Owen-Smith 1995, Dörgeloh 1998), using remote sensing (satellite images or aerial photos) (Fabricius & Coetzee 1992, Mace et al. 1999), using plots with Braun-Blanquet style cover-abundance coding (Ben-Shahar 1995), plotless sampling (Evans 1979) and sampling of vegetation at each observation point of observed animals (Ferrar & Walker 1974, Dekker et al. 1996, feeding site surveys: Watson & Owen-Smith 2000). Often, more than one of these techniques are used in conjunction. In addition, there exist a number of ways to determine the distribution of animals in their habitat and to analyse these observations statistically.

Brown (1988) used giving-up densities (GUD's) as an indication of habitat preference, predation risk and competition. Strictly speaking, both habitat and niche are measured to some extend by methods of optimal foraging that include interspecific competition. Patch use can be measure in four different ways (Brown 1988), including giving-up times (e.g. Ward & Seely 1996), total time spent in a patch, quitting harvest rates, and giving-up densities of resources (e.g. Kotler et al. 1994, Hughes et al. 1995). Field experiments with artificial or manipulated resources patches have two important advantages (Brown 1988): firstly foragers

remain in their natural environment and have the same alternative activities, predation risks and competition interactions and secondly, artificial patches permits the manipulation of variables of interest while the set of alternative activities remains the same. One problem in field studies with these methods is that they can't always distinguish between the species that used the resources (cf. Brown 1988).

Evans (1974) used six different methods to determine the distribution of animals in the environment. 1.He found the most useful method in the closed woodland of his study area to be the use of spoor and faecal pellets (with the help of an experienced tracker). A similar method was used by MacLeod et al. (1996). The main problem with this method is that spoor is more likely to be detected where a species is more mobile (which might not be in the preferred habitat). Therefore it doesn't truly measure relative densities. Temporal (e.g. daily) changes in habitat preferences also cannot be detected. 2.Vegetation drives were found most useful for detecting skulking species. Because different vegetation densities and visibility required different distances between people in the line, it was difficult to standardize. 3.Casual sightings were found useful for the presence of rare or localized species. It was also found to be difficult to standardize between habitats. 4.Another method consisted of dividing the area into 1 km square grids and surveying them for the presence of the different species. While this method gave some indication of the overall distribution of the different species, it didn't really show the vegetation type in which they occurred (e.g. if more than one vegetation type occurred in the same grid). Fabricius & Coetzee (1992) used smaller (200 x 200 m) grids that were surveyed on foot. Because landscape-scale factors were being considered, these grids might have been sufficient for discerning the different habitats at these scales. Ferrar & Walker (1974) also divided their study area into blocks, of which one or more were then searched each day on horseback or on foot and observations mapped. The grid approach was also used by Melton (1987) using 500 x 500 m grids. 5.Road transects (Ben-Shahar 1995, Dekker et al. 1996, Dörgeloh 1998, Mwangi & Western 1998, Perrin & Brereton-Stiles 1999, Winkler & Owen-Smith 1995) are relatively easy, but might sample only certain vegetation types (Evans 1979). 6.The last method used by Evans (1979) was to set up grids along game trails or at water-holes. Once again this didn't actually measure habitat use, but rather gave additional data on the number of individuals of a certain species using a particular trail or water-hole. Another method mentioned by Evans (1979), but not

actually used by him because of being impractical in closed woodland, is aerial surveying (Pettifer & Stumpf 1981). It is also possible to use large plots (100 to 180 ha) each evaluated in terms of different habitat factors such as soil properties and vegetation structure (e.g. Ben-Shahar & Skinner 1988, Beukes 1984). The number of animals observed in each can then be used to infer their habitat preference. Hansteen et al. (1997) used radio tracking (of root voles) to compare 3 different home range estimators. As was shown by Bayley et al. (1996), home range can simply be considered as habitat preference at a larger spatial and longer temporal scale. Telemetry was also used to determine the habitat preferences of grizzly bears at landscape scale (Mace et al. 1999). Although this method can show preference of certain areas and avoidance of others, it cannot determine the actual density distribution of animals. Therefore it can only use presence/absence data to indicate habitat preferences. Riney (1982) mentioned the possibility of using the size of home ranges as indication of habitat quality. Telemetry can be used to determine home range sizes (Hansteen et al. 1997). Frequently, different methods are combined (e.g. Evans 1979). The different methods might actually measure habitat choices made at different spatial and temporal scales. Because we cannot always know at which scales animals make their habitat choices, Ben-Shahar (1995) proposed and used a method where the same environmental variables are measured at different scales. The initial perception of habitat can then either be scaled down by subdividing habitats or scaled up by combining them. Statistical analysis can then be done using the data at these different scales. In this way it can be discerned when some variables are more important at a coarser scale while others are more important at a finer scale. MacLeod et al. (1996) used both faecal transects and strip transects on foot with observations of animals. One advantage of strip transects over road transects, is that on foot, transects can be chosen to include all the habitat types (MacLeod et al. 1996). Assuming that they will have the same preferences as wild animals, hand-reared, free-ranging individuals can be observed (e.g. Owen-Smith 1994) to determine their habitat preferences. This method can also be used at a finer scale to observe foraging preferences.

Frequently, multivariate statistics are used to analyse the data from habitat studies (e.g. Ben-Shahar 1995, Dekker et al. 1996 and Dörgeloh 1998 used correspondence analysis). Ben-Shahar (1995) also used Monte Carlo permutation tests to test for the statistical significance of the first canonical ordination axis. Ben-Shahar & Skinner (1988) combined multiple

regression analysis and correspondence analysis, demonstrating that they complement each other. They mentioned that the ideal analysis should be one that matches the perception of the animals. This is difficult in practice because the different factors might influence habitat choice at different spatial and temporal scales. In the study by Ben-Shahar & Skinner (1988) they postulated that where the two analysis methods differed, it indicates situations where some compromise is made by animals between the different factors that are important for them. Owen-Smith (1994) also used regression analysis. One of the earlier uses of multivariate techniques for examining large African herbivores was the use of Discriminant Function Analysis (DFA) by Ferrar & Walker (1974). Mwangi & Western (1998) used Detrended Correspondence Analysis (DCA). Chi-square analysis of goodness-of-fit is only used to test if animals show significant preference for some areas (Melton 1987, Winkler & Owen-Smith 1995, Dekker et al. 1996, MacLeod et al. 1996, Dörgeloh 1998, Watson & Owen-Smith 2000), but does not indicate for which areas there are significant preferences. Therefore this method is usually combined with other analyses. Melton (1987) used Bonferroni confidence intervals (cf. Winkler & Owen-Smith 1995, Watson & Owen-Smith 2000) as well as the S index (McNaughton 1978) to indicate selectivity. Analysis of Variance (ANOVA) as well as Kruskal-Wallis ANOVA for non-parametric data was used by MacLeod et al (1996, cf. the use of nested ANOVA by Owen-Smith 1994 and the combination of ANOVA with Tukey test by Watson & Owen-Smith 2000). Perrin & Brereton-Stiles (1999) used the G-Test (Zar 1974). The probability of occurrence of a certain habitat preference index can also be calculated directly from fitting a Pearson curve to the observed data (Pettifer & Stumpf 1981). Fabricius & Coetzee (1992) used a Geographic Information System (GIS) together with an Artificial Intelligence technique known as iterative dichotomising. This model (similar to decision trees) resulted in an expert system that could be used to predict the presence or absence of mountain reedbuck. A GIS was also used together with logistic regression for analysis of female grizzly bear habitat preference by Mace et al. (1999).

Evans (1979) mentions the importance of the group size in the different species for analysis. The individuals in a pair, small group or large herd of animals cannot be considered as separate observations, especially where these social bonds are permanent in nature. On the other hand a temporary “herd” that formed simply because of the congregation of many

animals in a patch of high quality, could be considered as separate individuals. This emphasizes the importance of knowing the behaviour of the animal species in habitat preference studies. Hansteen et al. (1997) highlighted the importance of spatiotemporal scale on autocorrelation. The classical example would be where a second observation of the same animals is recorded as a separate observation whereas they might be in the observed habitat only because of its proximity to the area where the first observation was taken (i.e. they have not had enough time to move away).

Habitat and sustainable stocking rates

If an ideal free distribution (Fretwell & Lucas 1970) is assumed, the distribution of the animals in the different available habitats can be used to determine a sustainable stocking density (Van Gils et al. 2004). Hobbs & Hanley (1990) caution that this can be done only if the underlying mechanism(s) driving the density distribution through the habitats are clear. If we assume that diet quality determines habitat quality, faecal analysis can be used to directly assess the quality of an area. This method assumes that diet quality determines the faecal contents. This relationship has been used and has been shown to be true for a large number of herbivores (Erasmus et al. 1978, Grant et al. 1995, MacLeod et al. 1996, Wrench et al. 1997, Grant et al. 2001).

Because of the problems associated with the carrying capacity concept and also because determination of sustainability requires long time spans, this study proposes that habitat preferences be used instead (Pienaar 1974) to determine the numbers of a certain species to introduce to an area (Dekker et al. 1996). A study of habitat preferences in one location will only give answers for locations with similar habitats elsewhere. If the preferred habitat occurs in the area considered for introduction, it will give an indication that at least those areas are suitable for the herbivore species concerned. Of course there will probably be habitats in the new area that didn't occur where the original preference study was done, but which might be preferred even more by the introduced species. In this case habitat studies would still give an estimate of the minimum area that will be suitable and thus a conservative estimate of the number of animals to begin with. Geographic Information Systems (GIS) have been shown to be useful for mapping and analyzing habitat preferences of large mammals (Fabricius &

Coetzee 1992, Mace et al. 1999). This approach was followed to study the habitat preferences of Bontebok in the Bontebok National Park.

Study Area

The original Bontebok National Park (BNP) was established in 1931 in the Bredasdorp district. By this time there were only about 17 Bontebok left (Barnard & Van der Walt 1961), giving an indication of how close to extinction this subspecies was. The bontebok population subsequently grew, but wouldn't increased beyond about 100, because of a copper deficiency (causing "swayback") and high parasite infestations (especially lungworm, *Protostrogylus* spp.) (Barnard & Van der Walt 1961). This, coupled with the area of that park being too small (676 ha) and 80% covered by unpalatable Renosterbos (*Elytropappus rhinocerotis*)(Van Rensburg 1975), led to the transfer of 84 Bontebok to the present Bontebok National Park in 1960. Of these, 61 Bontebok survived the transfer. In their new home the numbers grew to a high of over 400 in 1981, with a present population of about 230.

The present Bontebok National Park is situated south of Swellendam (34°03'19" S, 20°28'24" East). It borders on the Breede River in the South and has a fenced area of about 2800 ha. Recently, another 700 ha was acquired, but because it has not been fenced yet, is not included in this study. Also excluded is a thin strip south of the Breede River.

The BNP receives rain throughout the year, but normally more in autumn and winter (March to August). The mean annual rainfall (from data for 1961-1980 & 1991-2003) is 526 mm. Summers are warm to hot (temperatures seldom higher than 40°C) and winters are cool to mild (seldom colder than 0°C).

More than 90% of the soils in BNP consist of alluvium and gravel terraces (Theron 1967), mostly on 3 gravel terraces (higher than 120m in North-West, 80-100 m in the Northern and middle areas and about 65 m above sea-level in the East and South-East). The soils of these terraces are all sandy, with rounded stones and boulders sometimes constituting more than 50% of the volume. The alluvial soil occurs in the western plain below 80m above sea level, has a sandy loam to clayey texture and has almost no stones.

The vegetation of BNP can be classified as False Macchia (Acocks type 70) and Coastal Renosterveld (Acocks type 46) (Grobler & Marais 1967). According to the Broad Habitat Units of Cowling & Heijnis (2001) the northern two-thirds of the Park consists mostly of Suurbrak Grassy Fynbos en the Southern third of Overberg Coastal Renosterveld. According to Rebelo (1996), the third of the BNP that consists of Coastal Renosterveld comprises the largest conserved patch of this vegetation type. Grobler & Marais (1967) did a subjective vegetation classification of the BNP in terms of floristic composition, expected reaction to different treatments, and soil types. They found 13 different vegetation communities that could broadly be grouped into three groups, the sweetveld/renosterveld group, the mixed grassveld/*Leucadendron* communities (= grassy fynbos) and the tree communities. In general, the grassy fynbos can be found on the gravel terraces while the renosterveld occurs on the more fertile alluvium. Unfortunately, this study didn't include all of the present Bontebok National Park, being restricted to the older western part.

In addition to about 230 Bontebok, other larger ungulates in the BNP include about 35 Grey Rhebok (*Pelea capreolus*), about 20 Red Hartebeest (*Alcelaphus buselaphus*) and about 20 Mountain Zebra (*Equus zebra*).

Aims and hypotheses

One population of Bontebok (*Damaliscus pygargus pygargus*) was studied in one location (Bontebok National Park). The study had a number of objectives:

- Determine sustainable stocking densities for Bontebok in the Bontebok National Park (BNP) – addressed in Chapter 2.
- Determine which habitats in the Park are preferred – addressed in Chapter 2.
- Find the factors determining preference for those habitats – addressed in Chapter 3.
- Using all of the above information, give pragmatic advice to management at the BNP and also for the re-introduction of Bontebok in new areas – addressed in Chapter 4.
- Assess the usefulness of the methods used, and indicate priorities for further research – addressed in Chapter 3 & 4.

Five alternative hypotheses were proposed to explain a non-random density distribution:

1. Spatial differences in diet quality,

2. Predator avoidance strategies,
3. Intra-specific social interactions,
4. A combination of food and water requirements,
5. A combination of all the above factors.

These different factors were taken into account to try and understand the driving factors behind Bontebok spatial distribution in the BNP and thus avoid the pitfalls of using only animal densities that are mentioned in Hobbs & Hanley (1990) and in Van Horne (1983).

References

BAILEY, D.W., GROSS, J.E., LACA, E.A., RITTENHOUSE, L.R., COUGHENOUR, M.B., SWIFT, D.M. & SIMS, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386-400.

BARKER, R.D. 1986. An Investigation into the accuracy of herbivore diet analysis. *Australian Wildlife Research* 13: 559-568.

BARNARD, P.J. & VAN DER WALT, K. 1961. Translocation of the bontebok (*Damaliscus pygargus*) from Bredasdorp to Swellendam. *Koedoe* **4:** 105-109.

BARTELS, G.B., NORTON, B.E. & PERRIER, G.K. 1993. An Examination of the Carrying Capacity Concept. pp. 89-103 *In:* Behnke, R.H. Jr., I. Scoones & Kerven, C. (eds). Range Ecology at Disequilibrium. Overseas Development Institute, London.

BEGON, M., HARPER, J.L., & TOWNSEND, C.R. 1996. Ecology: individuals, populations and communities 3rd Edition. Blackwell Science, Oxford.

BEHNKE, R.H. JR. & SCOONES, I. 1993. Rethinking range ecology: Implications for rangeland management in Africa. pp. 1-30 *In*: Behnke, R.H. Jr., I. Scoones & Kerven, C. (eds). Range Ecology at Disequilibrium. Overseas Development Institute, London.

BEHNKE, R.H. JR., SCOONES, I. & KERVEN, C. (eds) 1993. Range ecology at disequilibrium: New models of natural variability and pastoral adaptation in African savannas. Overseas Development Institute, London.

BELL, R.H.V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. pp. 193-216 *In*: Huntley, B.J. & Walker, B.H. (eds). Ecology of tropical savannas. Springer Verlag, Berlin.

BEN-SHAHAR, R. 1995. Habitat classification in relation to movements and densities of ungulates in a semi-arid savanna. *African Journal of Ecology* 33: 50-63.

BEN-SHAHAR, R. & J.D. SKINNER. 1988. Habitat preferences of African ungulates derived by uni- and multivariate analyses. *Ecology* 69: 1479-1485.

BEUKES, P.C. 1984. Some aspects of the ecology of the Grey Rhebok (*Pelea Capreolus*, Forster 1790) in the Bontebok National Park. MSc Thesis, University of Stellenbosch, Stellenbosch. [In Afrikaans with English abstract]

BOSHOFF A.F., KERLEY, G.I.H. & COWLING, R.M. 2001. A pragmatic approach to estimating the distributions and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions* 7: 29-43.

BOUGHEY, A.S. 1968. Ecology of Populations. Macmillan, New York.

BRITS, J., VAN ROOYEN, M.W. & VAN ROOYEN, N. 2000. Technique to study the impact of large herbivores on woody vegetation within piospheres. *Koedoe* 43: 47-56.

BROOKS P.M., J. HANKS & J.V. LUDBROOK. 1977. Bone Marrow as an index of condition in African ungulates. *South African Journal of Wildlife Research* 7: 61-66.

BROWN, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22: 37-47.

CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. *Applied Biology* 1: 183-246.

COWLING, R.M. & HEIJNIS, C.E. 2001. The identification of broad habitat units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African Journal of Botany* 67: 15-38.

DANCKWERTS, J.E. 1989. Animal performance. pp. 47-53 *In*: Danckwerts JE. & Teague, W.R. (eds). Veld management in the eastern Cape. Department of Agriculture and Water Supply, Pretoria.

DEAN, W.R.J., HOFFMAN, M.T., MEADOWS, M.E. & MILTON, S.J. 1995. Desertification in the semi-arid Karoo, South Africa: review and reassessment. *Journal of Arid Environments* 30: 247-264.

DEKKER, B., VAN ROOYEN, N. & BOTHMA, J. DU P. 1996. Habitat partitioning by ungulates on a game ranch in the Mopani veld. *South African Journal of Wildlife Research* 26: 117-122.

DE LEEUW, P.N. & TOTHILL, J.C. 1993. The concept of rangeland carrying capacity in sub-Saharan Africa - myth or reality. pp. 77-88 *In:* Behnke, R. H. Jr., Scoones, I. & Kerven, C. (eds). Range ecology at disequilibrium. Overseas Development Institute, London.

DHONDT, A.A. 1988. Carrying capacity: a confusing concept. *Acta Oecologica* 9: 337-346.

DÖRGELOH, W.G. 1998. Habitat selection of a roan antelope (*Hippotragus equinus*) population in Mixed Bushveld, Nylsvlei Nature Reserve. *South African Journal of Wildlife Research* 28: 47-56.

DU TOIT, P.C.V. 2000. Estimating grazing index values for plants from arid regions. *Journal of Range Management* 53: 529-536.

EAST R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* **22:** 245-720.

ELLIS, J.E. & SWIFT, D.M. 1988. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. *Journal of Range Management* 41: 450-459.

ERASMUS, T., PENZHORN, B.L. & FAIRALL, N. 1978. Chemical composition of faeces as an index of veld quality. *South African Journal of Wildlife Research* 8: 19-24.

EVANS, P.G.H. 1979. Habitat preferences of ungulates in closed savanna of central Africa. *Mammal Review* 9: 19-32.

FABRICIUS, C. & K. COETZEE. 1992. Geographic information systems and artificial intelligence for predicting the presence or absence of mountain reedbuck. *South African Journal of Wildlife Research* 22: 49-55.

FERRAR, A.A. & WALKER, B.H. 1974. An analysis of herbivore/habitat relationships on Kyle National Park, Rhodesia. *Journal of South African Wildlife Management Association* 4: 137-147.

FRETWELL, S.D. & LUCAS, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19:** 16-36.

FYNN, R.W.S. & O'CONNOR, T.G. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology* 37: 491-507.

GRANT, C.C., MEISSNER, H.H. & SCHULTHEISS, W.A. 1995. The nutritive value of veld as indicated by faecal phosphorous and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. *Koedoe* 38: 17-31.

GRANT, C.C., PEEL, M.J.S., ZAMBATIS, N. & VAN RYSSEN, J.B.J. 2001. Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range & Forage Science* 17: 81-92.

GROBLER, P.J. & MARAIS, J. 1967. The vegetation of the National Bontebok Park. *Koedoe* **10:** 132-146. [In Afrikaans with English abstract]

GROSSMAN, D., HOLDEN, P.L. & COLLINSON, R.F.H. 1999. Veld management on the game ranch. pp. 261-279 *In*: Tainton, N. M. (ed.). Veld Management in South Africa, University of Natal Press, Pietermaritzburg.

HALL, L.S., KRAUSMAN, P.R. & MORRISON, M.L. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25: 173-182.

HANSTEEN, T.L., ANDREASSEN, H.P. & IMS, R.A. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimates. *Journal of Wildlife Management* 61: 280-290.

HARDY, M.B., HURT, C.R. & BOSCH, O.J.H. 1999. Veld condition assessment: Grassveld. pp.195-207 *in*: Tainton, N. M. (ed). Veld Management in South Africa. University of Natal Press, Pietermaritzburg.

HEADY, H.F. 1975. Rangeland management. McGraw-Hill Book Company. New York.

HOBBS, N.T. & HANLEY, T.A. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54: 515-522.

HOBBS, N.T. & SWIFT, D.M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49: 814-822

HUGHES, J.J., WARD, D. & PERRIN, M.R. 1995. Effects of substrate on foraging decisions by a Namib desert gerbil. *Journal of Mammalogy* 76: 638-645.

JARMAN, P. J. & A.R.E. SINCLAIR. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. pp.130-163 *In*: Sinclair, A.R.E. & M. Norton-Griffiths (eds). Serengeti: Dynamics of an ecosystem. University of Chicago Press, Chicago.

JONES, R.J. & SANDLAND, R.L. 1974. The relation between animal gain and stocking rate – Derivation of the relation from the results of grazing trials. *Journal of Agricultural Science, Cambridge* 83: 335-342.

KOTLER, B.P., GROSS, J.E. & MITCHELL, W.A. 1994. Applying patch use to assess aspects of foraging behavior in Nubian Ibex. *Journal of Wildlife Management* 58: 299-307.

LEOPOLD, A. 1961. Game Management. Charles Scribner's Sons, New York. (Reprint of 1933 book).

LI, S.G., HARAZONO, Y., OIKAWA, T., ZHAO, H.L., HE, Z.Y. & CHANG, X.L. 2000. Grassland desertification by grazing and the resulting micrometeorological changes in Inner Mongolia. *Agricultural and Forest Meteorology* 102: 125-137.

LINDENMAYER, D.B. & R.C. LACY. 2002. Small mammals, habitat patches and PVA models: a field test of model predictive ability. *Biological Conservation* 103: 247-265.

MACARTHUR, R.H. & WILSON, E.O. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-378.

MACE, R.D., WALKER, J.S., MANLEY, T.L., AKE, K., & WITTINGER, W.T. 1999. Landscape Evaluation of Grizzly Bear Habitat in Western Montana. *Conservation Biology* 13: 367-377.

MACLEOD, S.B., KERLEY, G.I.H., & GAYLARD, A. 1996. Habitat and diet of bushbuck *Tragelaphus scriptus* in the Woody Cape Nature Reserve: observations from faecal analysis. *South African Journal of Wildlife Research* 26: 19-25.

MCALLISTER, H.J. 1967. A quantitative faecal analytical investigation of the grazing preferences of impala (*Aepyceros m. melampus Licht.*). MSc Thesis, University of Natal, Pietermaritzburg.

MCLEOD, S. R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542.

MCNAUGHTON, S.J. 1978. Serengeti ungulates: Feeding selectivity influences the effectiveness of plant defense guilds. *Science* 199: 806-807.

MCNAUGHTON, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* 124:863-886.

MELTON, D.A. 1987. Habitat selection and resource scarcity. *South African Journal of Science* 83: 646-651.

MENTIS, M.T. 1977. Stocking rates and carrying capacity for ungulates on African rangelands. *South African Journal of Wildlife Research* 7: 89-98.

MUYA, S.M. & OGUGE, N.O. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. *African Journal of Ecology* 38: 62-71.

MWANGI, E.M. & WESTERN, D. 1998. Habitat selection by large herbivores in Lake Nakuru National Park, Kenya. Biodiversity and *Conservation* 7: 1-8.

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

NOVELLIE, P. 1987. Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe* 30: 1-17.

OBA, G., STENSETH, N.C. & LUSIGI, W.J. 2000. New perspectives on sustainable grazing management in arid zones of sub-Saharan Africa. *Bioscience* 50: 35-51.

OWEN-SMITH, N. 1994. Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. *Ecology* 75: 1050-1062.

OWEN-SMITH, N. & NOVELLIE, P. 1981. What should a clever ungulate eat*? American Naturalist* 119: 151-178

PEEL, M.J.S., BIGGS, H. & ZACHARIAS, P.J.K. 1998. The evolving use of stocking rate indices currently based on animal number and type in semi-arid heterogeneous landscapes and complex land-use systems. *African Journal of Range & Forage Science* 15: 117-127.

PERRIN, M.R. & R. BRERETON-STILES. 1999. Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *South African Journal of Wildlife Research* 29: 72-80.

PETTIFER, H.L. & STUMPF, R.H. 1981. An approach to the calculation of habitat preference data: Impala on Loskop Dam Nature Reserve. *South African Journal of Wildlife Research* 11: 5-13.

PIENAAR, U. DE V. 1974. Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 17: 185-195.

REBELO, A.G. 1996. South & South-West Coast Renosterveld. In: Low, A.B. & Rebelo, A.G. (Eds), Vegetation of South Africa, Lesotho and Swaziland (veg63.htm). Department of Environmental Affairs and Tourism, Pretoria.

RINEY, T. 1982. Study and management of large mammals. John Wiley & Sons, Chichester.

ROOKMAAKER, L.C. 1991. The scientific name of the Bontebok. *Zeitschrift für Säugertiekunde* 56: 190-191.

ROSENZWEIG, M.L. 1985. Some Theoretical Aspects of Habitat Selection. pp. 517-540 *In:* Cody, M.L. (ed). Habitat selection in birds. Academic Press, London.

SCHMIDT, A.G., THERON, G.K. & VAN HOVEN, W. 1995. A comparison of some methods used to estimate grazing capacity of a game ranch in Northern Province, South Africa. *Koedoe* 38: 123-128.

SEIDL, I. & TISDELL, C.A. 1999. Carrying capacity reconsidered: from Malthus' population theory to cultural carrying capacity. *Ecological Economics*. 31: 395-408.

SHARKEY, M.J. 1970. The carrying capacity of natural and improved land in different climatic zones. *Mammalia* 34: 564-572.

SKEAD, C.J. 1980. Historical mammal incidence in the Cape Province Volume 1. The Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town.

STUTH, J.W., FREER, M., DOVE, H. & LYONS, R.K. 1999. Nutritional management of free-ranging livestock. pp.696-751 *in*: Jung, H.G. & Fahey, G.C. Jr. (eds). Nutritional ecology of herbivores. Proceedings of the Vth International Symposium on the nutrition of herbivores. American Society of Animal Science, Savoy, Illinois, USA.

TAINTON, N.M. (ed). 1999. *Veld management in South Africa*. University of Natal Press. Pietermaritzburg.

THERON, J.M. 1967. The geology of the Bontebok Park, District Swellendam. *Koedoe* 10: 147-148. [In Afrikaans with English abstract]

TROLLOPE, W.S.W., TROLLOPE, L.A. & BOSCH, O.J.H. 1999. Glossary. *In*: Tainton, N. M. (Ed.) Veld Management in South Africa, University of Natal Press, Pietermaritzburg.

VAN GILS, J.A., EDELAAR, P., ESCUDERO, G. & PIERSMA, T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104: 197-204.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

VAN RENSBURG, A.P.J. 1975. The history of the National Bontebok Park, Swellendam. *Koedoe* 18: 165-190. [In Afrikaans with English abstract]

VESEY-FITZGERALD, D.F. 1960. Grazing succession among East African game animals. *Jounal of Mammalogy* 41: 161-172.

VIRGÓS, E. 2001. Role of isolation and habitat quality in shaping species abundance: a test with badgers (*Meles meles* L.) in a gradient of forest fragmentation. *Journal of Biogeography* 28: 381-389.

VORSTER, M. 1999. Veld condition assessment: Karoo. pp. 207-214 *in*: Tainton, N. M. (ed). Veld Management in South Africa. University of Natal Press, Pietermaritzburg.

WARD, D. & SEELY, M.K. 1996. Competition and habitat selection in Namib desert tenebrionid beetles. *Evolutionary Ecology* 10: 341-359.

WATSON, L.H. & OWEN-SMITH, N. 2000. Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology* 38: 130-137.

WESTOBY, M., WALKER, B. & NOY-MEIR, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42: 266-274.

WHITTAKER, R.H., LEVIN, S.A. & ROOT, R.B. 1973. Niche, habitat, and ecotope. *American Naturalist* 107: 321-338.

WILSON, D.E. & REEDER D.M. (Eds). 1993. Mammal species of the world. Smithsonian Institute Press, Washington DC.

WINKLER, A. & OWEN-SMITH, N. 1995. Habitat utilisation by Cape mountain zebras in the Mountain Zebra National Park, South Africa. *Koedoe* 38: 83-93.

WRENCH, J.M., MEISSNER, H.H. & GRANT, C.C. 1997. Assessing diet quality of African ungulates from faecal analyses: the effect of forage quality, intake and herbivore species. *Koedo*e 40: 125-136.

ZAR, J.H. 1974. Biostatistical Analysis. Prentice-Hall,London.

Habitat preferences and stocking densities of Bontebok in the Bontebok National Park. I. Factors affecting their distribution.

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Abstract

The carrying capacity concept has been controversial and a number of researchers have suggested that it be dropped. However, management of herbivores on natural veld requires some indication of the number of animals that can be kept sustainably without deterioration of the veld. A Geographic Information System was used to determine the habitat preferences of the rare Bontebok *Damaliscus pygargus pygargus* in the Bontebok National Park. The social classes of Bontebok showed different habitat preferences. Bontebok habitat preferences also differed from those of the other larger herbivores in the Bontebok National Park. Time since last fire, vegetation type and distance to permanent water were all identified as influencing bontebok habitat preferences.

Keywords: Bontebok, *Damaliscus dorcas dorcas*, *Damaliscus pygargus pygargus*, carrying capacity, habitat preferences, GIS, sustainable, stocking rates

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INTRODUCTION

For the re-introduction of game animals, one recurring question concerns the carrying capacity of the area for the species in question. However, the term ‘carrying capacity’ can have more than one meaning (Heady 1975, Caughley 1976, Dhondt 1988, De Leeuw & Tothill 1993) and the idea of a single, fixed carrying capacity might not be applicable in variable environments (e.g. McLeod 1997). We use the term "sustainable stocking rates" to indicate that more than one stocking density can be sustainable, but also that these densities are not constant in time.

Because of the problems associated with the carrying capacity concept and also because determination of sustainability requires long time spans, this study proposes that habitat preferences be used instead to determine the numbers of a certain species to introduce to an area (Pienaar 1974). If an ideal free distribution (Fretwell & Lucas 1970) is assumed, the distribution of the animals in the various available habitats can be used to determine a sustainable stocking density (Van Gils et al. 2004). Different quality habitats will have different animal densities reflecting their inherent capacity to sustain these observed densities. Hobbs & Hanley (1990) caution that this can be done only if the underlying mechanism(s) driving density distribution across habitats are clear. A study of habitat preferences in one location will only provide solutions for locations with similar habitats elsewhere. If there are habitats in the new area that did not occur where the original preference study was done, the minimum area that will be suitable could still be estimated. Even if there are higher quality habitats than in the original study area, a conservative estimate of the number of animals to stock will be given. One method used to determine habitat preferences is to map the observed distribution of animals using a Geographic Information System (GIS) and analyse this spatially explicit data with an expert system or more conventional multivariate statistics (e.g. logistic regression, discriminant function analysis) (Fabricius & Coetzee 1992, Mace et al. 1999).

The Western Cape province of South Africa used to have large numbers of large herbivores and predators (Skead 1980). Most of them have gone extinct locally and one species (*Hippotragus leucophaeus*) and one subspecies (*Equus quagga guagga*) have gone extinct. Recently, a number of the larger herbivores have been re-introduced in areas where they had gone extinct, including Bontebok (*Damaliscus pygargus pygargus,* Pallas 1766, formerly known as *Damaliscus dorcas dorcas* cf. Rookmaaker 1991, Wilson & Reeder 1993). Most of the landscape has been

transformed through ploughing with most of the natural vegetation left in areas of lower agricultural value (Rebelo 1996). Nutritional deficiencies such as was experienced in the previous location of the Bontebok National Park (Barnard & Van der Walt 1961), have raised concerns over the potential of this region to sustain large herbivores. The only larger herbivore species to survive in the area was the Bontebok (Skead 1980, Van Rensburg 1975). The Bontebok is considered rare (Wilson & Reeder 1993), but survived because of protection efforts, including a national park set up for this purpose (Bontebok National Park, near Swellendam, Western Cape). Research into its habitat preferences can have important conservation implications by providing guidelines for future re-introductions of Bontebok to its natural habitat. This study had a number of objectives:

1. Estimate sustainable stocking densities for Bontebok in the Bontebok National Park (BNP).
2. Determine which habitats in the Park are preferred.
3. Ascertain the factors determining preference for those habitats.
4. Assess the usefulness of the methods used, and indicate priorities for further research.
5. Give pragmatic advice for the management of Bontebok in the BNP as well as for the re-introduction of Bontebok.

In this article, the first two objectives are addressed while the last three objectives are considered in another manuscript (Luyt & Ward: Habitat preferences and stocking densities of Bontebok in the Bontebok National Park. II. Predictive Dempster-Schafer models of habitat selection.). The habitat factors that were suggested by previous studies (Pienaar 1974, Van Zyl 1978, Novellie 1987) as possible influences on the bontebok habitat preferences were: 1) vegetation types, 2) vegetation structure, 3) fire history, and 4) distance to permanent water.

METHODS

Study Area

The original Bontebok National Park was established in 1931 in the Bredasdorp district. By this time there were only about 17 Bontebok left in the wild (Barnard & Van der Walt 1961). The bontebok population subsequently grew, but did not increase beyond about 100, because of a copper deficiency (causing “swayback”) and high parasite infestations (especially lungworm, *Protostrogylus* spp.) (Barnard & Van der Walt 1961). This, coupled with the limited area of that park (676 ha) and the fact that much of it (80%) was covered by unpalatable Renosterbos (*Elytropappus*

rhinocerotis)(Van Rensburg 1975), led to the transfer of 84 Bontebok to the present Bontebok National Park in 1960. Of these, 61 Bontebok survived the transfer. In their new home, the numbers grew to a high of over 400 in 1981 with a present population of about 230.

The present Bontebok National Park is situated south of Swellendam (34°03'19" S, 20°28'24" East). It borders on the Breede River in the South and has a fenced area of about 2800 ha. Recently, another 700 ha was acquired, but because it has not been fenced yet, is not included in this study. Also excluded is a thin strip south of the Breede River (See Figure 1).

The BNP receives rain throughout the year, with more in autumn and winter (March to August). The mean annual rainfall (from data for 1961-1980 & 1991-2003) is 526 mm. Summers are warm to hot (temperatures seldom higher than 40°C) and winters are cool to mild (seldom colder than 0°C).

More than 90% of the soils in BNP consist of alluvium and gravel terraces (Theron 1967). Most of the park consists of three gravel terraces (higher than 120 m in North-West, 80-100 m in the Northern and middle areas and about 65 m above sea-level in the East and South-East)(see Figure 1). The soils of these terraces are all sandy, with rounded stones and boulders sometimes constituting more than 50% of the volume. The alluvial soil occurs in the western plain below 80 m above sea level, has a sandy loam to clayey texture and has almost no stones.

The vegetation of BNP can be classified as False Macchia (Acocks type 70) and Coastal Renosterveld (Acocks type 46) (Grobler & Marais 1967). According to the Broad Habitat Units of Cowling & Heijnis (2001) the northern two-thirds of the Park consists mostly of Suurbrak Grassy Fynbos and the southern third of Overberg Coastal Renosterveld. Grobler & Marais (1967) did a subjective vegetation classification of the BNP in terms of floristic composition, expected reaction to different treatments such as fire, and soil types. They found 13 different vegetation communities that could broadly be grouped into three groups, the sweetveld/renosterveld group, mixed grassveld/*Leucadendron* communities (= grassy fynbos) and the tree communities. In general, the grassy fynbos can be found on the gravel terraces with renosterveld on the more fertile alluvium.

In addition to about 230 Bontebok, other larger ungulates in the BNP include about 35 Grey Rhebok (*Pelea capreolus*), about 20 Red Hartebeest (*Alcelaphus buselaphus*) and about 20 Mountain Zebra (*Equus zebra*).

Methods

Long-term stocking rates for Bontebok in the BNP were calculated from historical data, both from the literature and from the records of South African National Parks (SANP). The method is essentially the same as that used by Sharkey (1970) and East (1984) among others, who included the effects of rainfall and soil nutrient status in their calculations. It amounts to counting the biomass/numbers of animals occurring naturally in an area over a long period, and using the mean value as the carrying capacity. This value can be correlated with rainfall and then be used to adapt this mean carrying capacity for a certain year (but cf. East 1984 for the interaction effect of different soil types and the different effects on different herbivore species).

From January to December 2003, the same 38 km road transect (see Figure 1) was repeated monthly (21 times in all) to determine the density distribution of bontebok in the BNP representative of all seasons (Hall et al. 1997). When an animal was observed, the compass direction to the animal, the distance to the animal and the Cartesian coordinates of the observer were recorded with a Geographic Positioning System (GPS). Herds were recorded as one observation, with the animal closest to the middle of the herd taken as representative and the number of animals in the herd counted. Where possible, sex and age were also noted. Three age classes of Bontebok were distinguished, viz. kids (lambs), juveniles (yearlings) and adult. Herds of free-ranging males and immature females ("bachelors") were also differentiated from territorial herds (cf. David 1973). The activity of the animals during the observation was recorded. For comparison purposes, three other species in the BNP, viz. Grey Rhebok (*Pelea capreolus*), Red Hartebeest (*Alcelaphus buselaphus*), and Mountain Zebra (*Equus zebra*) were also observed in the same way. Because of visibility problems, observations were only taken when it was not raining. The resulting data were read into a GIS for further analysis. Downloading and re-projecting GPS data was done with Waypoint+ version 1.8.03. All data, when not already in this projection, was projected to Universal Transverse Mercator (Datum WGS84 zone 34 S). Some initial processing and projecting of vector maps were done in MapInfo (cf. Clarke 2001). All subsequent GIS work was done in GRASS (Geographic Resources Analysis Support System), a GIS running on Linux (Clarke 2001). In GRASS, a map

was drawn of all the points where animals had been seen. The transect used for observations was also tracked by GPS and read into the GIS. The range finder used for determining the distance to the animals, decreased in precision as the distance increased, with a precision of about 50 m for distances greater than 400 m, but was accurate even to the nearest meter for animals closer than 50 m. Therefore, a buffer zone of 400 m around the transect was used in the GIS as the area of interest. This buffer was then adapted to take into account the topography and other visibility factors of the BNP (cf. Figure 1). This area could be used to determine the basic density of all the observed animals. Because of the precision error of the rangefinder, Landsat satellite images (with a pixel size of only 30 m x 30 m) were found to be acceptable for mapping the habitat.

The vegetation study of Grobler & Marais (1967) was taken as a starting point for habitat definition. Thirteen 5 m x 20 sample vegetation plots were used to see if the vegetation communities had remained essentially the same in plant species composition and spatial extent. Sampling was mostly restricted to dominant species, grasses, and the occasional rare or conspicuous plant. Thereafter a Landsat 7 TM (Thematic Mapper) image from the summer of 1999/2000 was used to determine if these vegetation types could be distinguished on the Landsat image. It consisted of TM bands 5, 4 and 8 (corresponding to short wave infrared SWIR1 (1.55-1.75μm), very near infrared VNIR (0.78-0.90μm) and panchromatic (0.52-0.90μm)), which were used as red, green and blue respectively to form a false colour image. Using ground control points from GPS data that were acquired during data collection, the image was geo-referenced in GRASS.

Using unsupervised (maximum-likelihood clustering) classification, followed by supervised classification, the vegetation types of Grobler & Marais (1967) could be extended to those areas of the BNP that were not included in the 1967 study. A number of 5 m x 5 m plots were taken for ground-truthing. Because of time constraints, and because vegetation was not the main focus of the study, this sampling was not done in every distinct vegetation type. Instead, a subjective general vegetation survey was done that was similar to Grobler and Marais' (1967) study. All plant samples were pressed, and digital pictures taken were entered into a custom database program. Overall, 250 plant species were found, but some were only identified to genus level.

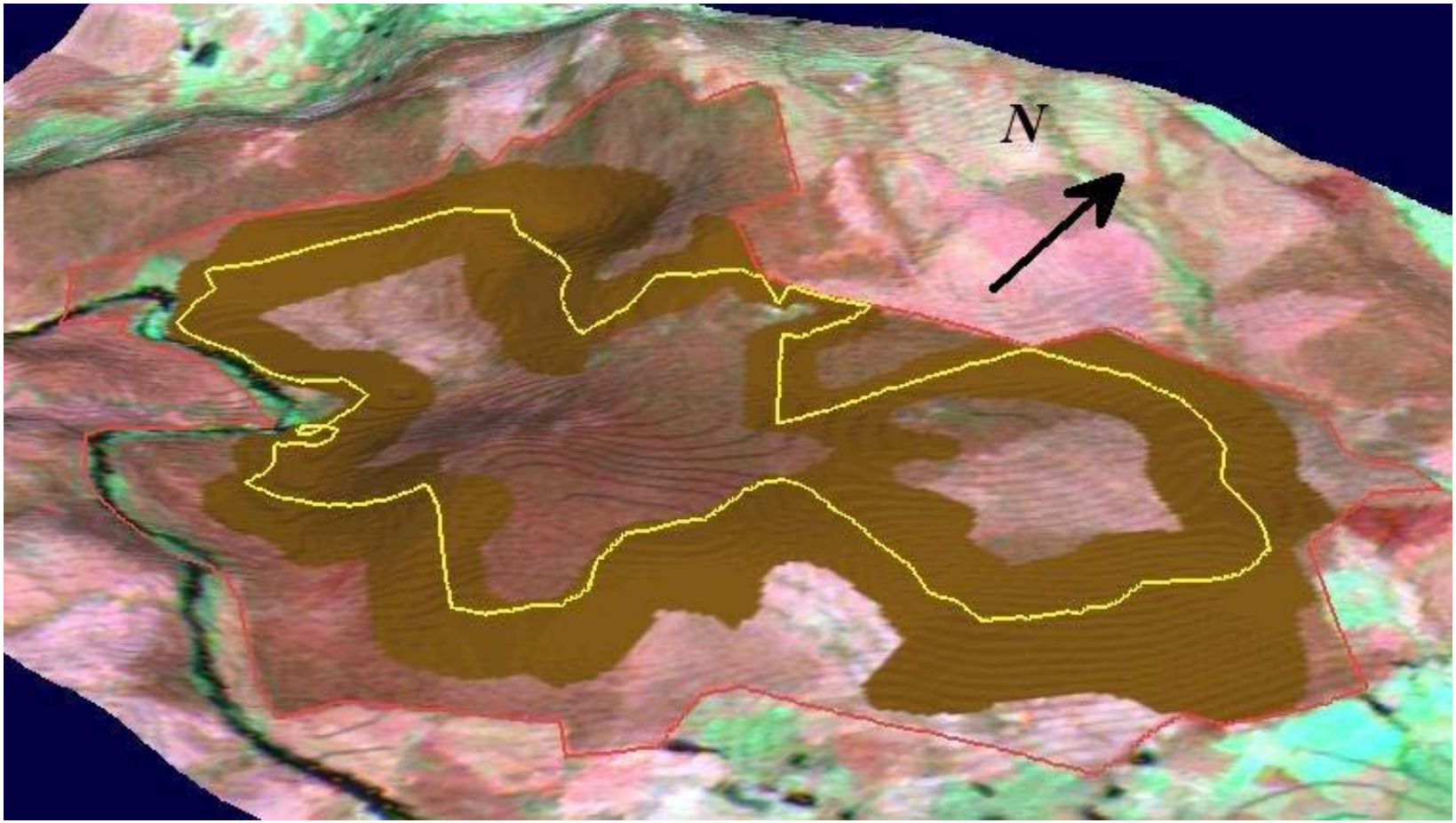

Figure 1 The topography of the Bontebok National Park, with the 2003 Park boundaries in red, and its effect on visibility. Only data from within the (brown) area visible from the transect (in yellow), was used. Visibility was determined both by topography and by vegetation. Fynbos typically occurred on the higher altitudes with Renosterveld more in the lower southwestern area (cf. Figure 4).

Because different electro-magnetic radiation frequencies give different information about vegetation condition, they have been combined in different vegetation indices, each with its own characteristics. The most commonly used vegetation index is the NDVI (Price et al. 2002, Hosseini et al. 2004), used to give an overall indication of living plant biomass. It is given by (Near Infrared – Red)/(Near Infrared + Red), which is equivalent to (TM4 – TM3)/(TM4 + TM3). Because the red Landsat band was not available in this case, (TM4/TM8+TM4) was used instead as a simpler and faster alternative to the vegetation analysis. It produced an output map with a continuous range of values, which were then grouped together in discrete classes for the purpose of analysis.

Other habitat factors to be mapped were: 1) Permanent water points (from GPS readings), 2) Topography (Digital Elevation Model (DEM) as well as slope and aspect maps (cf. Figure 1) were created in GRASS from a contour map), 3) Fire (fire blocks were mapped from GPS tracks, and their fire history acquired from the BNP management). Five groups were differentiated according to the year of last fire: burnt pre-1999, 1999, 2001, 2002 and 2003. Because vegetation was clearly correlated with soil type (Grobler & Marais 1967), soil was not mapped as a separate factor. However, the vegetation index probably included some soil reflectance together with vegetation information.

Statistical analysis was done in Microsoft Excel 2000, using the Resampling Stats Excel Add-in version 2.0 for Windows (Simon 1995), as well as Statistica 6.1. From the GIS, values for each factor (vegetation type, vegetation index, distance to water, and fire history) were determined for each observation and the density of animals in each area calculated. For all data, a Kolmogorov-Smirnov test (Lilliefors option) was used to test for normality. To determine if the different species were distributed differently in the BNP, a Kruskal-Wallis ANOVA by ranks was done. Because the data were projected to UTM, the test could be done on the actual X and Y values. A number of observations from the previous year (2002) were compared to 2003 using a Mann-Whitney U-test. The same test was also used to compare the distributions in two seasons (rainy vs. dry) and to compare the distribution of the territorial breeding herds to that of the non-breeding free-ranging “bachelor” herd (cf. David 1973). To test if the different factors had an influence on the density distribution, a permutation test (resampling/rerandomization, Lunneborg 2000) was done using the absolute mean difference between each level and the grand mean. Shuffling within rows was

used because repeated measures (transects) were used to collect the data. Where the data were normally distributed, repeated measures ANOVA could be used instead. For each species, the tests were repeated for 1) habitat type, 2) vegetation index class, 3) fire, and 4) distance to permanent water. Because water was expected to be only important in summer in this winter rainfall region (Van Zyl 1978), this effect was tested for observations from the dry season only. The temporal effect of fire was tested using a χ^2test to compare 2002 and 2003 in terms of fire. The significance of the individual levels was tested with a bootstrap procedure using Resampling Stats (Simon 1995).

RESULTS

Sustainable stocking densities

From the historical data (De Graaff et al. 1976), it is known that there was natural population growth in Bontebok from 1960 until 1972. From 1973 onward, animals were periodically removed and the population size was mostly kept between 200 and 250. If we consider only the period of natural population growth (Figure 2), the curve can be seen to flatten after a 1969 high of 294 to average at about 275. This number could be considered the Ecological Carrying Capacity, as defined by Caughley (1976). A number of regression analyses were run on the available historical data to test for correlations between area affected by fire (ha), rainfall (mm) and population size or lambing percentage. The only significant correlation ($p < 0.05$) was found between rainfall and lambing percentage of the next year. However, the effects were rather weak ($r^2 = 0.29$).

Distribution pattern

There was a significant difference in the distribution of Bontebok between 2002 and 2003 (Mann-Whitney U = 9054.00, $p<0.01$), with a shift from East to West. The density distribution of the animals also differed among species (Kruskal-Wallis H = 14.4, $p<0.01$ for X values; Kruskal-Wallis H = 17.8, $p<0.01$ for Y values; cf. Figure 3) with Red Hartebeest were observed more to the West than either Bontebok or Mountain Zebra (Grey Rhebok observations had an East-West overlap with all the other species $p > 0.05$) and Mountain Zebra more to the South than any of the other species. No significant difference could be detected in the distribution of Bontebok between seasons ($p>0.05$). On the other hand, there was a significant difference in the

spatial distributions of the territorial herds and the "bachelors" (Mann-Whitney U = 48739.5, $p<0.001$), with the breeding herds observed more frequently in the West.

The above results did not include the size of the herds seen, but only their distribution. To test for the effects of the different factors on the densities of the animals, the relative availability of each area for each factor was determined in GRASS.

Habitat types

For determining the vegetation types, the unsupervised clustering analysis (maximum-likelihood analysis) resulted in 35 spectral classes. There was a high level of heterogeneity. For example, the *Leucadendron-Stipagrostis* plant communities were shown as a mosaic of at least three different colours. Therefore, supervised classification was also used, resulting in the vegetation map in Figure 4. Because the ground-truthing was done only in the areas visible from the transect, some areas of the map remain with unknown vegetation types. Overall, a similar distribution of plant communities to that of Grobler & Marais (1967) was found. Some communities changed a little in spatial extent (e.g. the *Erica diaphana* community). In others, a change in dominant plant species was found (e.g. the *Cliffortia ruscifolia* community of Grobler & Marais (1967) was found to be dominated by *Leucadendron salignum* and a tall *Passerina* sp.). Some of the communities of Grobler & Marais (1967) were subdivided. Thus, the larger patches of *Cynodon dactylon* were mapped separately, because their importance as bontebok habitat was shown by evidence that they were created and/or maintained as grazing lawns (McNaughton 1984, Person *et al*. 2003). A few vegetation types were new (e.g. *Muraltia hysteria* shrubland). In all, 25 different habitat types were found.

Using the vegetation index, we produced a simpler map with only 6 classes. Although strictly speaking, these classes were simply indices of reflectance, some link to general vegetation structure could be seen. The classes ranged from "Dense, Green, Grassy" through "Sparse, Dry, Shrubs" to "Dense, Trees" (See Figure 5).

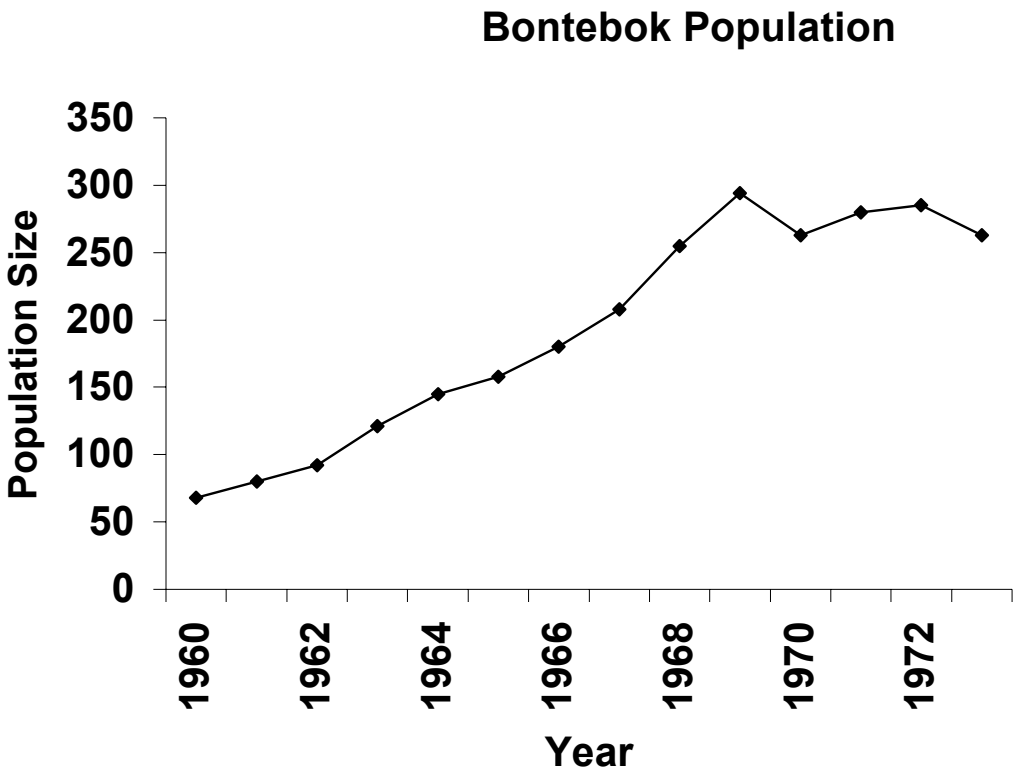

Figure 2 Population growth of Bontebok in BNP after the relocation. Population size appears to stabilize after 1969 between 250 and 300 animals.

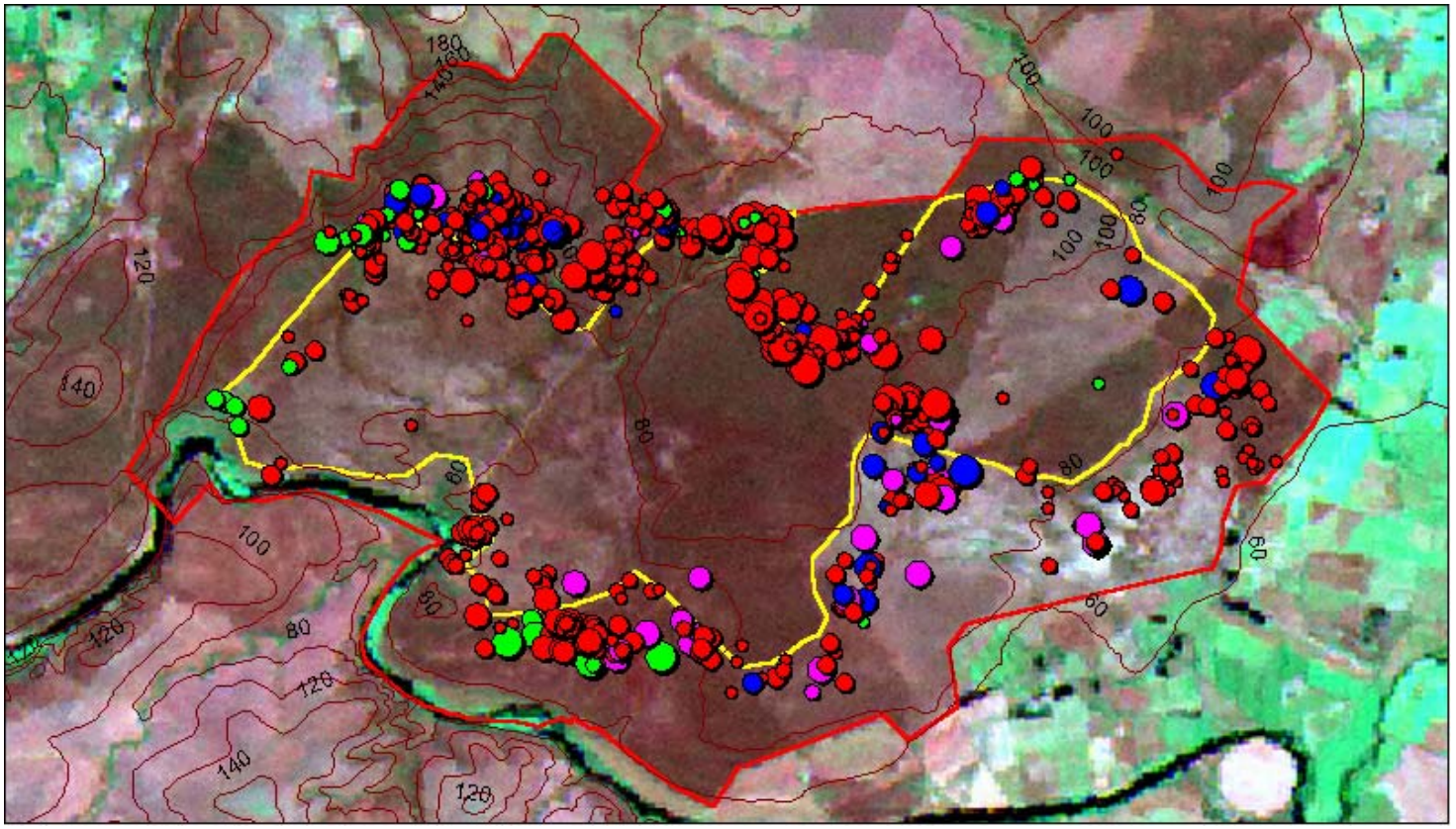

Figure 3 Observations of all animal species in the Bontebok National Park. Clearly visible is the lighter area in the East that burnt in 1999. The park boundary is given in red and the basic transect used for observations in yellow. The size of the coloured circles represents only the relative size of the herd. Both herd size and number of herds would determine the density of animals when divided by the area in which they were observed. Red Hartebeest (Green) were seen more frequently in the West compared to the other species. Mountain Zebra (purple) was seen more frequently in the South than the other species. Grey Rhebok (Blue) and Bontebok (Red) were mostly seen in the same areas.

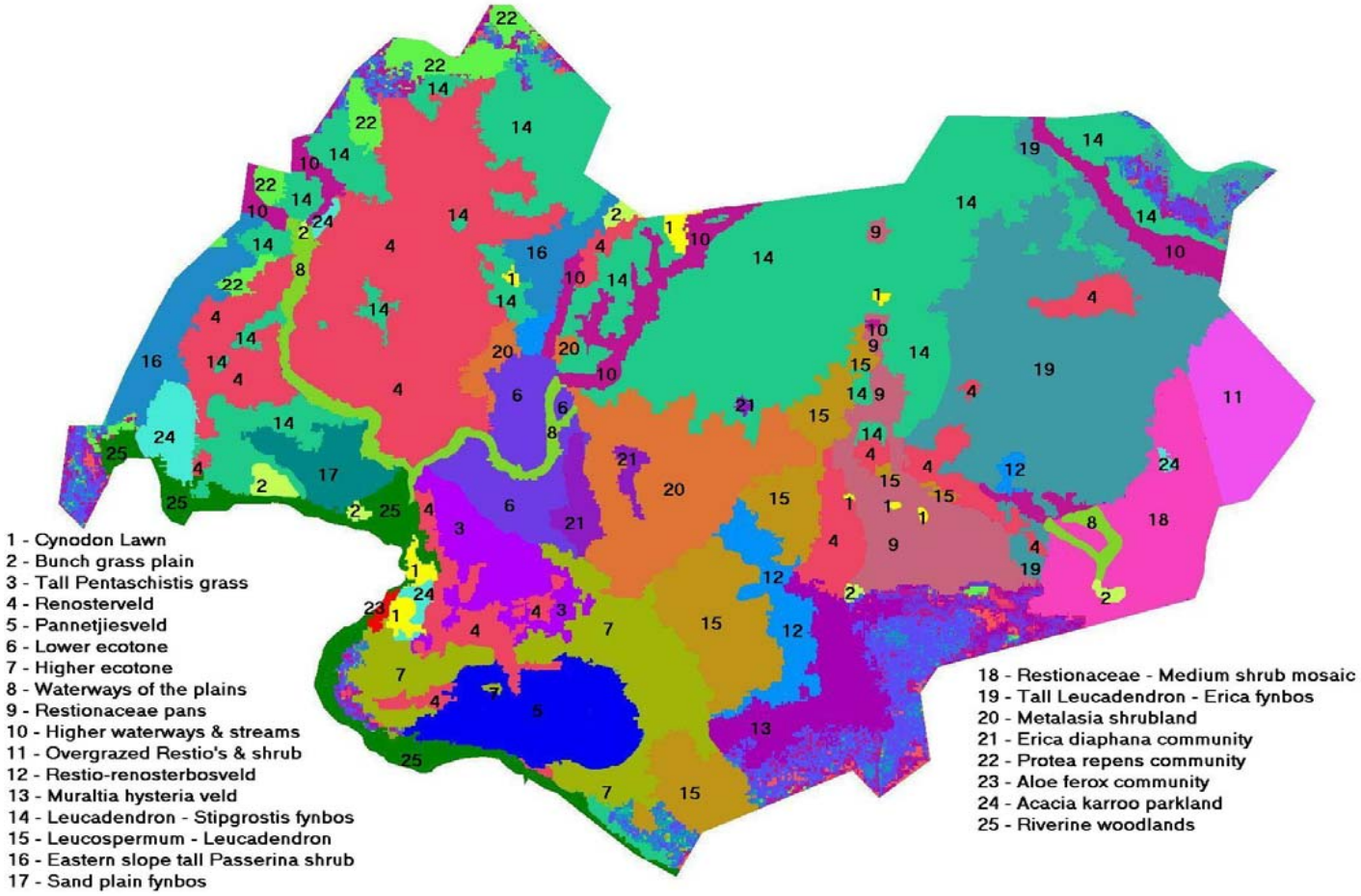

Figure 4 Vegetation (Habitat) types of Bontebok National Park. Some areas further away from the transect remain unidentified. In the main, the vegetation types were consistent with those of Grobler & Marais (1967).

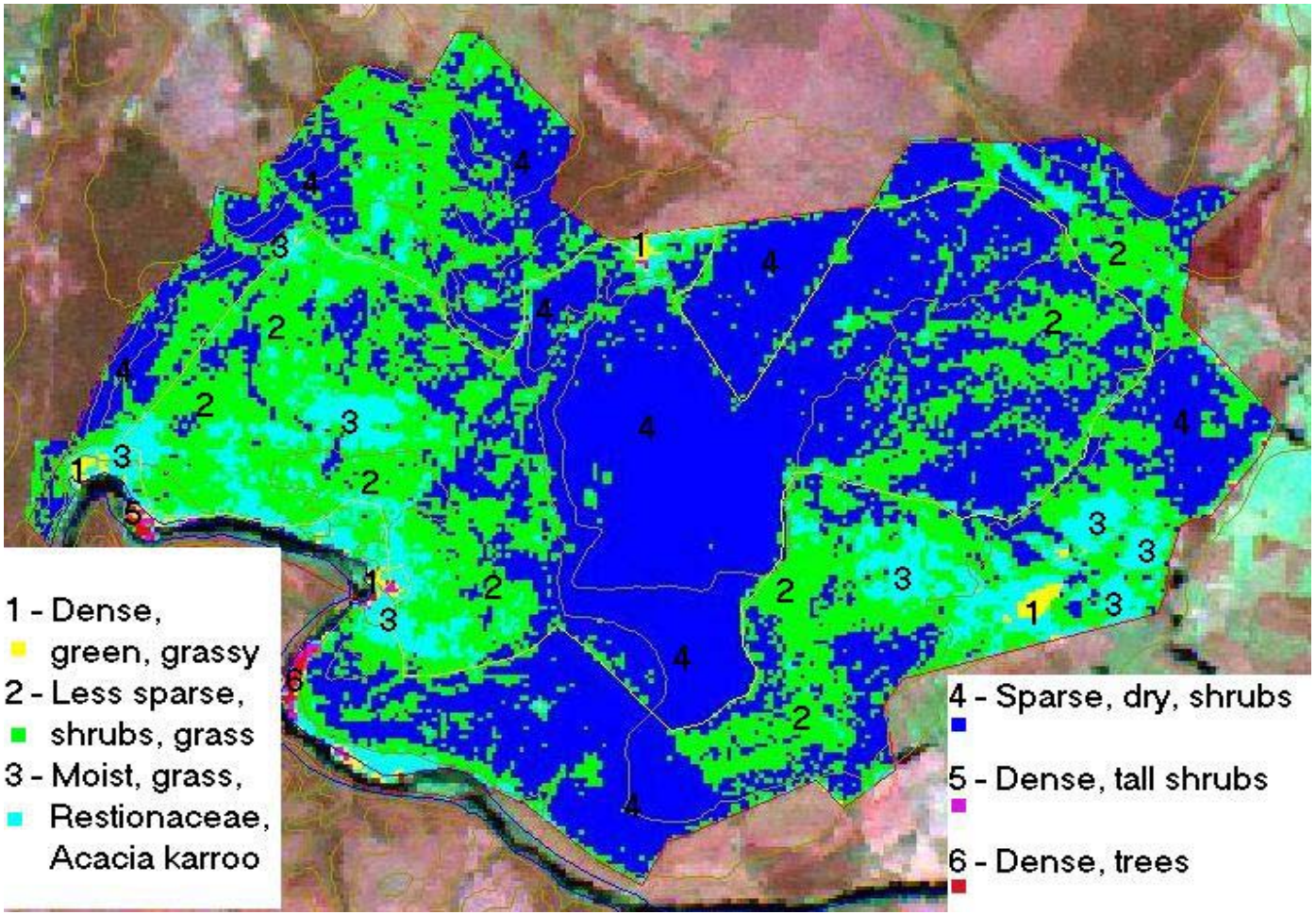

Figure 5 The vegetation index classes (TM4/TM8+TM4). No significant preference for any of these index classes by Bontebok could be shown. Grey Rhebok avoided the open grassy patches and the short dense shrubs and grass (Class 2) (p=0.025, resampling: 10000 iterations).

Fire effects on density distribution

Because it was previously shown that four years after a fire, Bontebok no longer show preference for that area (Novellie 1987), all areas burnt before 1999 were grouped together and a fire map produced from the historical data (Figure 6). For all these maps, a mask of the buffer zone around the transect (Figure 1) was used to produce areas restricted to those visible from the transect from which the GIS could be used to calculate the observed densities in each area.

The densities of the Bontebok were calculated and resampling tests used to determine if they differed significantly between areas. The areas that burnt in 2003 (youngest veld) had significantly higher bontebok densities than the overall mean ($p<0.001$, p value calculated by resampling, 10000 iterations) and higher reproductive output (mean number of kids/herd)($p<0.01$, p value calculated by resampling, 10000 iterations). The areas that burnt in 1999 and before had a significantly lower ($p=0.0014$, p value calculated by resampling, 10000 iterations) than average density of Bontebok (cf. Table 1). Overall, fire had a significant positive effect ($p<0.001$, p value calculated by resampling, 10000 iterations) on Bontebok density distribution.

Fire also had a significant positive effect ($p<0.001$, p value calculated by resampling, 10000 iterations) on Red Hartebeest, but here the effects were less clear. The area that burnt in 2002 ($p=0.02$, p value calculated by resampling, 10000 iterations) as well as the old veld that burnt before 1999 ($p<0.001$, p value calculated by resampling, 10000 iterations), had a significantly higher than average hartebeest density. In addition, the areas that burnt in 1999 ($p=0.036$, p value calculated by resampling, 10000 iterations) and 2001 ($p=0.007$, p value calculated by resampling, 10000 iterations) had significantly lower than average hartebeest densities.

Mountain zebra had some similarity in their density distribution when compared to Red Hartebeest, but here the pattern was a bit clearer with an overall significant effect ($p=0.01$, p value calculated by resampling, 10000 iterations). Veld burnt in the previous year was preferred ($p<0.001$, p value calculated by resampling, 10000 iterations) and there was a total avoidance of the small area that was burnt in 2001 and subsequently heavily grazed by Bontebok ($p=0.026$, p value calculated by resampling, 10000 iterations).

Table 1 Effects of fire on densities (animals/ha) of all herbivores. . Significant p-values indicated by asterisk (*). The column headings show the year of last fire. The effect on territorial Bontebok was similar to that of all Bontebok. The density of kids produced in the most recent burnt area was significantly higher than the mean of the older blocks (p = 0.0015, p value calculated by resampling, 10000 iterations). Grey Rhebok had a similar pattern to that of Bontebok (preference for younger veld), but the effect was not significant overall (p = 0.055, p value calculated by resampling, 10000 iterations). No consistent effect of fire on Red Hartebeest was detected. Mountain Zebra preferred veld that burnt in the previous year, whereas the overgrazed veld from the 2001 burn was avoided.

All Bontebok	**2003**	**2002**	**2001**	**1999**	**pre-1999**	**Overall**
Observed mean density:	0.165	0.080	0.046	0.027	0.016	0.067
p :	< 0.0001*	0.403	0.182	0.0085*	0.0014*	< 0.0001*
Bontebok kids						
Observed mean density:	0.0061	0.0033	0.0009	0.0018	0.0015	0.0027
p :	0.0015*	0.598	0.082	0.381	0.226	0.007*
Grey Rhebok						
Observed mean density:	0.0189	0.0030	0.0098	0.0084	0.0005	0.0081
p :	0.0168*	0.252	0.716	0.947	0.088	0.052
Red Hartebeest						
Observed mean density:	0.0079	0.0184	0.0003	0.0024	0.0226	0.0103
p :	0.503	0.0205*	0.0072*	0.0367*	0.0006*	0.0001*
Mountain Zebra						
Observed mean density:	0.007	0.021	0.000	0.009	0.003	0.008
p :	0.870	0.001*	0.026*	0.845	0.164	0.0105*

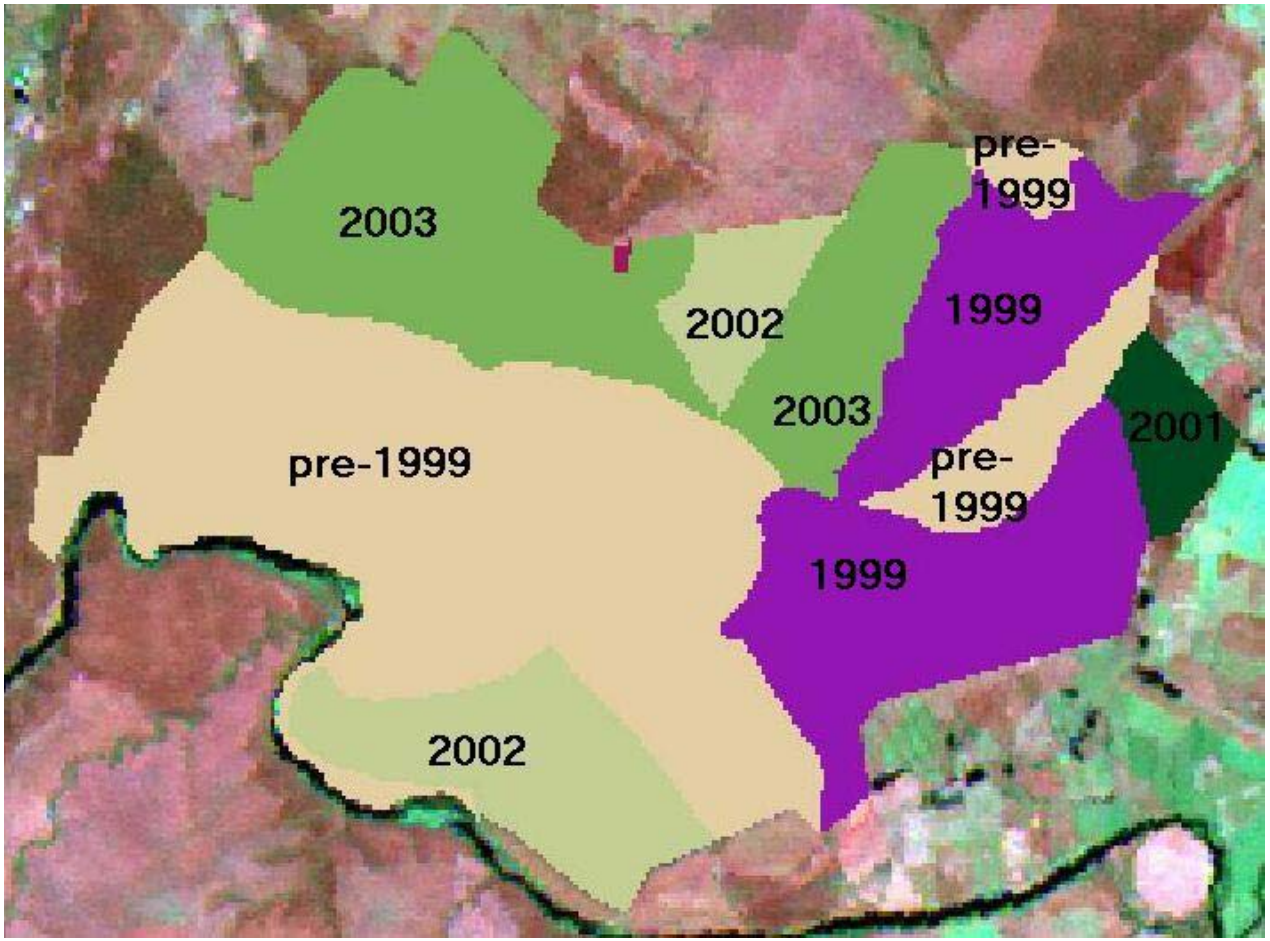

Figure 6 Fire map for BNP. Shown is the last year of fire. Note the small area that burnt in 2001. In the beginning of 2002 (until the 2002 burning, blocks were burnt in April) almost all the free-ranging bontebok were found in that 65 ha area (cf. Table 2).

Table 2 Contingency table showing the change in animal distribution because of fire. Given is the total number of animals of each species counted and expected in each fire block in 2002 and 2003. Asterisks indicate significant differences between them. In the last column, the p value of the χ^2test for each species and for each year is shown. Fire had a significant effect ($p<0.0001$) for all species. Subsequent bootstrap analysis showed for which fire blocks the observed numbers differed significantly from the expected. The expected value was calculated from the null hypothesis that animals will use areas according to availability (N expected =(size of area÷size of total area) x total number of animals observed). It should be noted that the 2002 data were collected in the beginning of the year, before the planned burn of 2002 and so the most recently burnt area was that of 2001 and not of 2002.

NUMBER OF ANIMALS		YEAR OF LAST FIRE					P-VALUE
SPECIES	YEAR	2003	2002	2001	1999	pre-1999	
BONTE-	**Observed: 2002**	41	4*	50*	10*	34*	< 0.0001*
BOK	***Expected: 2002***	*35*	*14*	*5*	*31*	*54*	
	Observed: 2003	1200*	232*	47*	175*	182*	< 0.0001*
	Expected: 2003	*467*	*186*	*65*	*410*	*708*	
HARTE-	**Observed: 2002**	10*	4*	0	0	0*	< 0.0001*
BEEST	***Expected: 2002***	*4*	*1*	*0*	*3*	*5*	
	Observed: 2003	47*	46*	0*	2*	24*	< 0.0001*
	Expected: 2003	*30*	*12*	*4*	*27*	*46*	
GREY	**Observed: 2002**	18*	0	4*	10	0*	< 0.0001*
RHEBOK	***Expected: 2002***	*8*	*3*	*1*	*7*	*12*	
	Observed: 2003	110*	7*	8	43	4*	<0.0001*
	Expected: 2003	*44*	*17*	*6*	*38*	*66*	
ZEBRA	**Observed: 2002**	15	0*	2	21	4	0.00015*
	Expected: 2002	*11*	*10*	*0*	*14*	*6*	
	Observed: 2003	43	49*	0*	45	25*	<0.0001*
	Expected: 2003	*41*	*16*	*6*	*36*	*62*	
ALL	**Observed: 2002**	84*	8*	56*	41	38*	< 0.0001*
SPECIES	***Expected: 2002***	*58*	*23*	*8*	*51*	*87*	
	Observed: 2003	1400*	334*	55*	265*	235*	< 0.0001*
	Expected: 2003	*583*	*232*	*81*	*511*	*882*	

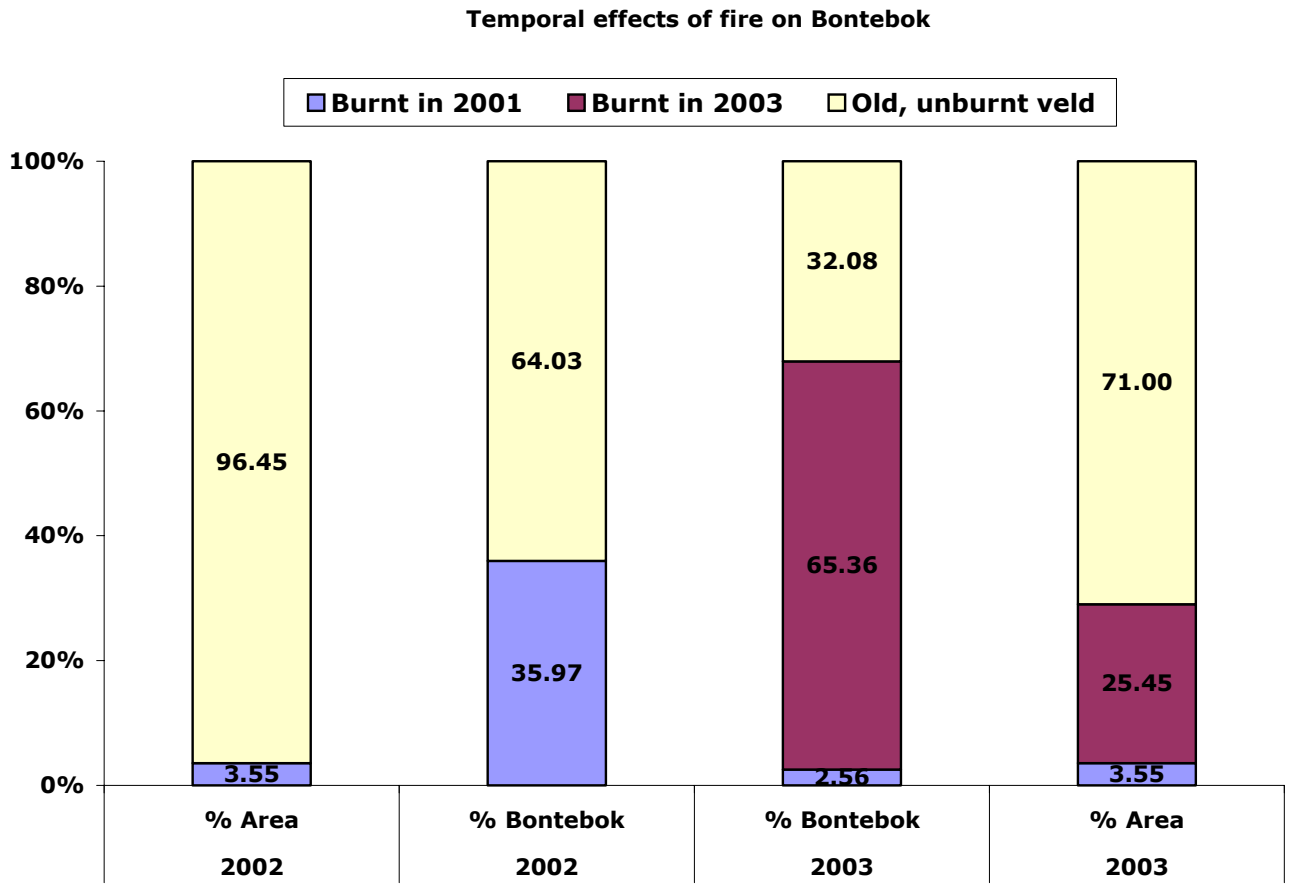

Figure 7 The change in Bontebok distribution due to fire. In both years a much greater percentage of Bontebok was found on the recently burnt area than the actual size of the area (as % of total area) would suggest.

Fire is the only one of the habitat factors considered that has a clear temporal effect. Some data from the beginning of 2002 were available and showed a clear shift in the distribution of the animals because of a change in fire (Table 2).

Bontebok changed between 2002 and 2003 from preferring the 2001-burnt area to the 2003-burnt area. Red Hartebeest changed from what was then old veld (only burnt in 2003) to the 1-year-old veld (2002) and pre-1999 fire areas. They appeared to prefer the area that burnt in 2002 both before and after the 2002 fire. Although Grey Rhebok did not show their 2002 preference for the 2001 burning block in 2003, they showed some preference prior to the fire for the area that burnt in 2003. No preference could be shown for the Mountain Zebra in 2002, but some avoidance of the area that was burnt later in that year was shown. By 2003 the same pattern as that of Table 1 was shown and this one-year-old veld became the preferred area.

Vegetation effects on density distribution

There was a significant effect of habitat type on Bontebok densities, with a preference for the more grassy vegetation types (cf. Table 3). In four vegetation types, i.e. habitats 20 – 23, no animals were observed. This was mainly because they were right at the edges of the visible strip around the transect, but also because all consisted of tall, woody vegetation with low visibility and/or occurred on steep slopes where a lower preference by Bontebok could be expected. They were excluded from all analyses.

Territorial males (the only ones to breed, according to David 1973) showed significantly above-average densities in only two vegetation types: *Cynodon dactylon* lawns (Habitat 1) and in the Restionaceae/Medium tall shrub Mosaic (Habitat 18) in the Eastern part of the BNP (cf. Table 8). It is possible that the observed preference for Habitat 18 was actually due to the proximity of a large grassy plain (a part of Habitat 2) that occurred inside Habitat 18. Several small grazing lawns (McNaughton 1984) were also included in this vegetation. Because of the smaller sample size, behavioural effects on the density distribution of the other animal species were not considered.

Table 3 Habitat types and their effects on Bontebok densities. In general, the *Cynodon dactylon* lawns, the Bunchgrass plains and the Restionaceae wetlands (Habitats 1, 2 and 9 on the vegetation map: Figure 4) had higher densities of Bontebok than the mean, whereas the Fynbos-Renosterveld lower ecotone (Habitat 6), the Sand Plain Fynbos (Habitat 17) and the *Acacia karroo* woodlands (Habitat 24) were avoided. The occurrence of grazing lawns significantly affected observed densities (p = 0.0082, p value calculated by resampling, 10000 iterations).

All Bontebok: **Habitat**	**P:**	**Mean Density:**	**Grazing lawns present:**
Cynodon lawn	< 0.0001*	0.327	*
Bunchgrass plain	0.019*	0.148	*
Pentaschistis grassy plain	0.056	0.010	
Renosterveld	0.908	0.073	*
Pannetjiesveld Mosaic	0.106	0.117	*
Fynbos-Renosterveld lower ecotone	0.048*	0.005	*
Renosterveld-Fynbos higher ecotone	0.288	0.034	
Lower water drainages (semi-wetlands)	0.188	0.027	
Restionaceae Wetlands	0.030*	0.139	*
Higher water drainages (Streams)	0.276	0.103	*
Short Restionaceae & Shrubs (Overgrazed)	0.999	0.068	*
Restionaceae Renosterbosveld	0.220	0.030	
Muraltia_hysteria Shrubland	0.227	0.030	
Leucadendron/Stipagrostis Fynbos	0.405	0.096	
Leucadendron/Leucospermum Shrubland	0.071	0.013	
Tall Passerina Shrubland (Eastern Slopes)	0.055	0.128	
Sand Plain Fynbos	0.043*	0.002	
Restionaceae/Medium high shub Mosaic	0.272	0.033	
Leucadendron/Erica Fynbos	0.058	0.011	
Acacia_karroo Woodland	0.048*	0.006	*
Riverine Woodlands	0.259	0.032	
OVERALL	< 0.0001*	0.068	

Table 4 The effect of permanent water points on Bontebok densities. In general, significantly higher densities ($p<0.01$) of Bontebok were found at intermediate distances from water points (550 m – 800 m). At distances farther than 1300 m from water, Bontebok were found at significantly ($p<0.05$) lower than average densities. In the wet season the general preference by Bontebok for intermediate distances to water continued. In the dry season, significantly higher than average ($p=0.025$**,** calculated by resampling, 10000 iterations) densities of Bontebok were found within 200 m from permanent water points.

Bontebok:	**All**		**Wet season**		**Dry season**	
Water distance:	**P:**	**Mean density**	**P:**	**Mean density**	**P:**	**Mean density**
0-200 m	0.949	0.067	0.121	0.039	0.025*	0.122
200-300 m	0.076	0.040	0.240	0.045	0.085	0.029
300-550 m	0.217	0.047	0.423	0.052	0.159	0.038
550-650 m	0.003*	0.111	0.0029*	0.118	0.144	0.096
650-800 m	0.0002*	0.125	0.0002*	0.138	0.108	0.100
800-1300 m	0.505	0.076	0.109	0.093	0.208	0.043
1300-1600 m	0.0395*	0.036	0.0039*	0.015	0.347	0.078
1600-2300 m	0.0075*	0.025	0.0139*	0.025	0.068	0.026
OVERALL	<0.0001*	0.066	<0.0001*	0.066	0.0179*	0.066

Red Hartebeest showed a significant ($p=0.0042$, calculated by resampling, 10000 iterations) preference for the Pannetjiesveld area (Habitat 5). Grey Rhebok showed no significant preference for any vegetation type ($p>0.05$, calculated by resampling, 10000 iterations). The Mountain Zebra, like the Grey Rhebok, showed no overall significant vegetation type preference ($p>0.05$, calculated by resampling, 10000 iterations).

One alternative indicator of habitat quality is the density of kids born in an area. For Bontebok, this indicated that breeding herds on short *Cynodon* lawns and on the bunchgrass plains (Habitats 1 & 2) had a higher reproductive success rate than in other habitats ($p<0.0001$, calculated by resampling, 10000 iterations).

The vegetation index was not significantly correlated with the Bontebok, Red Hartebeest or Mountain Zebra density distribution but was significantly correlated with Grey Rhebok density distribution ($p=0.025$**,** calculated by resampling, 10000 iterations), who avoided the areas with denser shrubs and grass.

Effects of water on density distributions

Distance to permanent water had a significant effect ($p<0.001$) on Bontebok density distribution (Table 12) with higher densities at intermediate distances and lower densities farther than 1300 m from water. The same pattern was found in the rainy season. However, in the dry season (October - March), there was a change in this distribution and significantly more Bontebok was found within 200 m of permanent water (Table 13). For all other species, distance to water did not have a significant effect on their density distribution.

DISCUSSION

Sustainable stocking densities

If the general assumptions of the carrying capacity concept are accepted, an "ecological carrying capacity" of about 0.098 animals per ha was found from historical data. However, this carrying capacity model does not adequately consider the possible long-term negative effects of the animals on the vegetation. The rainfall in the driest year was about 80% of the mean rainfall. To be safe, an average stocking density of about 80% of this "ecological carrying capacity" might therefore be better (but see Saltz et al. 2004). This gives a population size of 220 or a density of about 0.079 animals/ha, which is slightly less than the present population of about 230

animals. These stocking rates are probably sustainable because there has been relatively little change in the vegetation since the study by Grobler & Marais in 1967. This stocking density of 0.079 animals/ha (= 12.727 ha/animal) is a lot higher than the 22 ha/animal estimated by Boshoff et al. (2001).

Habitat preferences

The statistical tests show that Bontebok are not randomly distributed in the Bontebok National Park, but that different factors have different effects on their distribution. These results do not explain which factors are most likely to have the greatest effect on the habitat preferences of Bontebok. For this purpose we used predictive Dempster-Shafer models as described elsewhere (Luyt & Ward in prep.).

Bontebok showed a clear preference for recently burnt veld as well as significant avoidance of veld that burnt ≥ 4 years ago. A clear temporal shift of Bontebok distribution to areas of recent fire could be shown. The preferred vegetation types for Bontebok were: 1) *Cynodon dactylon* dominated lawn (Habitat 1), 2) bunchgrass plains (mostly *Eragrostis curvula* dominated) (Habitat 2) and 3) Restionaceae pans (Habitat 9). The large grass component of the Restionaceae pans helps to explain the preference by Bontebok. The two habitat types with below-average Bontebok densities, Lower Fynbos-Renosterveld ecotone and Sand plain Fynbos, both had tall shrubs (*Leucadendron salignum* and *Leucadendron linifolium* respectively) as dominant species, while their small grass component consisted mostly of tall *Stipagrostis zeyheri* that are not eaten by Bontebok when mature (Novellie 1987).

Van Horne (1983) defined habitat quality as a measure of survival, density and reproduction. Densities only were measured in this study. Although survival rates could not be compared directly between the different habitats, it was possible to determine if the general density distribution of Bontebok reflects real habitat quality by examining reproductive success rates in the different habitats. This showed that two of the preferred vegetation types, the *Cynodon dactylon* lawns (Habitat 1) and the bunchgrass plains (Habitat 2) had significantly higher than average densities of Bontebok kids.

The results of this study are consistent with those of Van Zyl (1978) who showed that Bontebok are generally independent of water in winter, but need to drink regularly in the dry, hot summer.

Whereas both Red Hartebeest and Mountain Zebra differed significantly from Bontebok in their observed distribution, a similar difference was not found for Grey Rhebok. These findings agree with those of Beukes (1984) who also found no difference in the habitat preference of Bontebok and Grey Rhebok. The most likely reason for this partial overlap is probably that there is almost no overlap in their diets (Beukes 1984) and therefore little or no competition (Bontebok diet consists of 97.5 % grass, while Grey Rhebok diet includes only 2.7% grass). It is also possible that the Bontebok and Grey Rhebok actually stay close to each other simply to increase the likelihood of observing predators. The other species differed from Bontebok in terms of fire, with both Red Hartebeest and Mountain Zebra preferring one-year-old veld. Red Hartebeest was the only one to show significant preference for a certain vegetation type, by being found in higher densities in the Pannetjiesveld Mosaic while permanent water had no significant effect on the density distribution of any of the other species.

The spatial scales used in this study could not be used to quantify the importance of smaller grazing lawns or individual plant species in the habitat preferences of Bontebok. Although lower level selection usually manifests on higher spatial levels as well (Bailey et al. 1996), it should be kept in mind that some lower-level spatial selection criteria might have been missed in the present study. This could be important if the results are used to identify areas of Bontebok habitat preference outside the BNP.

Acknowledgements

EL wishes to thank the personnel at Bontebok National Park for all their assistance and Swellendam Backbackers for providing sleeping facilities and space for data capture. To the Peace Park Foundation and Cape Nature Conservation for providing EL with the Landsat TM image, our sincerest thanks. Thanks also to Benjamin Walton for helping with plant identification. This material is based upon work supported by the National Research Foundation of South Africa under Grant number 2053674 to David Ward.

References

BARNARD, P. J. & VAN DER WALT, K. 1961. Translocation of the bontebok (*Damaliscus pygargus*) from Bredasdorp to Swellendam. *Koedoe* 4: 105-109.

BEUKES, P.C. 1984. Some aspects of the ecology of the Grey Rhebok (*Pelea Capreolus*, Forster 1790) in the Bontebok National Park. MSc Thesis, University of Stellenbosch, Stellenbosch. [In Afrikaans with English abstract]

BOSHOFF, A.F.,. KERLEY, G.I.H & COWLING, R.M. 2001. A pragmatic approach to estimating the distributions and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions* 7: 29-43.

CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. *Applied Biology* 1: 183-246.

CLARKE, K.C. 2001. Getting started with Geographic Information Systems. Prentice Hall, Upper Saddle River.

COWLING, R.M. & HEIJNIS, C.E. 2001. The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African Journal of Botany* 67(1): 15–38. (Electronic Arc/View .shp map acquired from Cape Nature Conservation)

DAVID, J.H.M. 1973. The behaviour of the bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift fur Tierpsychologie* 33: 38-107.

DE GRAAFF, G., VAN DER WALT P.T. & VAN ZYL, L.J. 1976. Population composition of the Bontebok *Damaliscus dorcas dorcas* in the Bontebok National Park during Januarie 1974. *Koedoe* 19: 67-74. [In Afrikaans with English abstract]

DE LEEUW, P.N. & TOTHILL, J.C. 1993. The concept of rangeland carrying capacity in sub-Saharan Africa - myth or reality. In: Behnke, R.H. Jr., Scoones. I. & Kerven, C. (Eds), Range ecology at disequilibrium (pp. 77-88). Overseas Development Institute, London.

DHONDT, A.A. 1988. Carrying capacity: a confusing concept. *Acta Oecologica* 9: 337-346.

EAST R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* 22: 245-720.

FABRICIUS, C. & COETZEE, K. 1992. Geographic information systems and artificial intelligence for predicting the presence or absence of mountain reedbuck. *South African Journal of Wildlife Research* 22: 49-55.

FRETWELL, S.D. & LUCAS, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

GROBLER, P. J. & MARAIS, J. 1967. The vegetation of the National Bontebok Park. *Koedoe* 10: 132-146. [In Afrikaans with English abstract]

HALL, L.S., KRAUSMAN, P.R. & MORRISON, M.L. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25: 173-182.

HEADY, H.F. 1975. Rangeland management. McGraw-Hill, New York.

HOBBS, N.T. & HANLEY, T.A. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54: 515-522.

HOSSEINI, S.Z., KHAJEDDIN, S.J. & AZARNIVAND, H. 2004. Application of ETM+ data for estimating rangelands cover percentage. XXth ISPRS Congress, Istanbul.

LUNNEBORG, C.E. 2000. Data Analysis by Resampling: Concepts and Applications. Duxbury, Pacific Grove.

MACE, R.D., WALKER, J.S., MANLEY, T.L., AKE, K. & WITTINGER, W.T. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* 13: 367-377.

MCLEOD, S.R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542.

MCNAUGHTON, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* 124:863-886.

NOVELLIE, P. 1987. Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe* 30: 1-17.

PERSON, B.T., HERZOG, M.P., RUESS, R.W., SEDINGER, J.S. ANTHONY, R.M. & BABCOCK, C.A. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecologia* 135: 583-592.

PIENAAR, U. DE V. 1974. Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 17: 185-195.

PRICE, K.P., GUO, X. & STILES, J.M. 2002. Optimal Landsat TM band combinations and vegetation indices for discrimination of six grassland types in eastern Kansas. *International Journal of Remote Sensing* 25: 1-12.

REBELO, A.G. 1996. South & South-West Coast Renosterveld. In: Low, A.B. & Rebelo, A.G. (Eds), Vegetation of South Africa, Lesotho and Swaziland (veg63.htm). Department of Environmental Affairs and Tourism, Pretoria.

ROOKMAAKER, L.C. 1991. The scientific name of the Bontebok. *Zeitschrift für Säugertiekunde* 56: 190-191.

SALTZ, D., WARD, D., KAPOFI, I. & KARAMATA, J. 2004. Population estimation and harvesting potential for game in arid Namibia. *South African Journal of Wildlife Research* 34: 153-161.

SHARKEY, M. J. 1970. The carrying capacity of natural and improved land in different climatic zones. *Mammalia* 34: 564-572.

SIMON, J.L. 1995. Resampling stats: User's guide. Resampling Stats Inc., Roseville.

SKEAD, C.J. 1980. Historical mammal incidence in the Cape Province Volume 1. The Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town.

THERON, J. M. 1967. The geology of the Bontebok Park, District Swellendam. *Koedoe* 10: 147-148. [In Afrikaans with English abstract]

VAN GILS, J.A., EDELAAR, P., ESCUDERO, G. & PIERSMA, T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104: 197-204.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

VAN RENSBURG, A.P.J. 1975. The history of the National Bontebok Park, Swellendam. *Koedoe* 18: 165-190. [In Afrikaans with English abstract]

VAN ZYL, L. J. 1978. The water requirements and drinking habits of Bontebok *Damaliscus dorcas dorcas* (Pallas, 1766) in the Bontebok National Park. MSc thesis. University of Stellenbosch, Stellenbosch. [In Afrikaans with English abstract]

WILSON, D.E. & REEDER D.M. (Eds). 1993. Mammal Species of the World. Smithsonian Institute Press, Washington DC.

Habitat preferences and stocking densities of Bontebok in the Bontebok National Park. II. Predictive Dempster-Schafer models of habitat selection.

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Abstract

A Geographic Information System (GIS) was used to determine the habitat preferences of Bontebok in the Bontebok National Park. To find the behavioural factors responsible for the observed density distribution, predictive Dempster-Shafer models were built into the GIS. Faecal samples were used to test if the GIS models actually corresponded to grazing quality. The predicted preference probabilities of the different models were then compared to the observed densities to determine the model with greatest predictive power. It was found that a model combining different behavioural factors gave the best prediction of habitat preferences. Taken separately, grazing quality had the greatest effect on habitat preferences.

Keywords: Bontebok, *Damaliscus dorcas dorcas*, carrying capacity, habitat preferences, GIS, sustainable, stocking rates, Dempster, Shafer, model

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INTRODUCTION

Hobbs & Hanley (1990) and Van Horne (1983) both emphasized that habitat quality cannot be deduced from simply examining the density distribution of animals. That is, higher density might not reflect better habitat quality. Indeed, it has been shown by Hobbs & Hanley (1990) that the concept of habitat quality determination is complex. For example, it is possible that one area might have higher production and nutritive values at low herbivore densities than a second, but be unable to sustain (because of biomass restrictions) the higher densities of animals that the "lower quality" habitat might support. In other words, the "high quality" habitat would then have a higher "economic carrying capacity" (Caughley 1976) than the "low quality" habitat, but a lower "ecological carrying capacity" than the "low quality" habitat. In this case, a subjective decision is required to term the high nutrition, low biomass habitat "high quality"; and the opposite definition could just as well be used. Van Horne (1983) defined habitat quality as a combination of survivability, reproduction and density. Hobbs & Hanley (1990) added that the management aims would also play a role in the definition of habitat quality. For this reason, it is important to understand the factors governing habitat choice (Van Horne 1983) when considering habitat preference and, in particular, when using animal density to measure it.

The Western Cape province of South Africa used to have large numbers of large herbivores and predators (Skead 1980, cf. Luyt & Ward: Habitat preferences and stocking densities of Bontebok in the Bontebok National Park. I. Factors affecting their distribution.). The only larger herbivore species to survive in the area (Skead 1980, Van Rensburg 1975) was the Bontebok (*Damaliscus pygargus pygargus,* Pallas 1766, formerly known as *Damaliscus dorcas dorcas* cf. Rookmaaker 1991, Wilson & Reeder 1993). The Bontebok is considered rare (Wilson & Reeder 1993), but survived because of protection efforts, including a national park set up for this purpose (Bontebok National Park, near Swellendam, Western Cape). Research into its habitat preferences can have important conservation implications by providing guidelines for future re-introductions of Bontebok to its natural habitat.

Assuming that Bontebok would show some preferences for certain areas (Luyt & Ward: Habitat preferences and stocking densities of Bontebok in the Bontebok National Park. I. Factors affecting their distribution.), it was hypothesized that the

behavioural factors causing the observed density distribution would be one of the following:

1. Spatial differences in diet quality,
2. Predator avoidance strategies,
3. Intra-specific social interactions,
4. A combination of food and water requirements,
5. A combination of all the above factors.

By considering the reasons for different habitat preferences, some of the pitfalls of using density as indicator of habitat preferences (Van Horn 1983, Hobbs & Hanley 1990) could be avoided.

METHODS

The study was done in the Bontebok National Park as described in an earlier paper (Luyt & Ward: submitted). Bontebok (*Damaliscus pygargus pygargus*) was the only species considered in this part of the study, which focuses on the driving factors behind their habitat preferences.

A predictive Dempster-Shafer model was built in the GIS for each alternative hypothesis. The Dempster-Shafer theory of evidence can be seen as a generalization of Bayesian probability (Shafer 1976) to better deal with uncertainty. It has been most widely used in Computer Science (Artificial Intelligence & Expert Systems) (Yager et al. 1994). It differs from Bayesian statistics mainly in the following areas: 1) Because of uncertainty, the subjective probability (belief) of a proposition A and the probability of its compliment A', need not have the Bayesian relationship A= 1- A'; 2) the probability P(B) used to update a present belief P(A|B) can be values other than 1 (it doesn't have to be a certainty), 3) there are no real prior and posterior probabilities, in the sense that different evidences can be combined in any order; 4) it makes provision for the combination of contradictory evidence (Shafer 1976).

For the model, probability values were given to each factor that was expected to be important for Bontebok habitat preference. These probabilities represented the degree of belief that a Bontebok density, greater than what would be expected from a random distribution, would be found in a certain place. For example, fire was expected to be important (Novellie 1987), with preference for younger veld. Therefore, vegetation older than 5 years was given a probability of 0.5 of being preferred, and with

increasing probabilities for younger vegetation so that vegetation younger than 1 year would have a probability of 0.9 of being preferred. The different factors contributing to the same alternative hypothesis were then combined using Dempster's rules of combination and conditioning (Shafer 1976).

A common assumption in such studies is that habitat preference and carrying capacity are determined by dietary constraints (e.g. prey density: Van Gils et al. 2004). Hobbs & Swift (1985) has shown that both diet quantity and quality are important for determining "carrying capacity". In drier sweetveld areas, defined as veld in which grazing has a similar quality in all seasons (Tainton 1999), it can be expected that diet quantity is more important. In more mesic, sourveld areas, defined as areas where grazing loses most of its nutritional value in the non-growing season (Tainton 1999), diet quality would become the restricting factor. In all likelihood there is probably a continuous change from quantity being the most important, changing towards quality being the most important. East (1984) has shown that the importance of veld quality differs for different species, because some species are more selective grazers and still find the most nutritious food in poor conditions whereas other, less selective species were negatively influenced by lower quality. Because nutrient quality (copper deficiency) had been a factor in the original Bontebok National Park (Barnard & Van der Walt 1961), it was considered as one of the alternative hypotheses to explain Bontebok habitat preference.

Fire (Novellie 1987, Rowe-Rowe 1982) was expected to influence food quality. Pienaar (1974) and Grunow (1980) showed that the closely related Blesbok (*Damaliscus pygargus phillipsi*) preferably graze on short grass. Surprisingly, Novellie (1987) showed that there was little preference for specific grass species, other than taller grass species being preferred shortly after fire (when they were still short), and shorter grass species preferred later on. Specific species were therefore not included in the model. All classes used on maps were converted to subjective probabilities that Bontebok will prefer a certain class. In general, it was assumed that shorter, grassier habitats would better fulfil Bontebok dietary requirements than tall, shrubbier ones, because Bontebok are known to be short-grass grazers (Pienaar 1974, Beukes 1984). Habitat types with more, shorter grass were therefore given higher probabilities and taller, woodier vegetation lower probabilities for above-average

Bontebok densities. Two Dempster-Shafer geographic models were created as probability maps for Bontebok preference when diet is the determining factor. The first combined only habitat type (Figure 4 in Luyt & Ward: submitted) and fire (Figure 6 in Luyt & Ward: submitted). The second (Figure 1) also combined the vegetation index map (Figure 5 in Luyt & Ward: submitted) with this habitat type-fire model. The vegetation index was included to compensate for some of the subjectivity involved in assigning probability values for vegetation types *a priori*. It was expected to reflect diet quality as well as quantity to some extent. These models were built before any of the results from the statistical analyses were available, so they are true predictive models and not *post hoc* "data dredging" methods (McNaughton 1999). To test if areas shown by these models as higher probabilities really had higher diet quality, the results of the faecal analysis were used (see below).

If we assume that diet quality determines habitat quality, faecal analysis can be used to directly assess the quality of an area. This method assumes that diet quality determines the faecal contents; this relationship has been used and shown to be true for a large number of herbivores (Erasmus et al. 1978, Grant et al. 1995, MacLeod et al. 1996, Wrench et al. 1997, Grant et al. 2001). Because no digestive system can absorb all nutrients from ingested food, food of a higher quality will result in faeces with a higher nutrient content (Grant et al. 2001). Faecal analysis has some advantages over other methods of determining diet quality. In contrast to methods that examine the available vegetation (Bodenstein et al. 2000, Muya & Oguge 2000, Watson & Owen-Smith 2000) no assumptions about diet selection need to be made, because the diet that is actually selected will produce the measured faecal nutrient content. Because species differ from each other in digestive efficiency, a regression equation between the nutrient quality in the ingested food and the faecal nutrient content is usually found for each species and nutrient in a controlled environment (Erasmus et al. 1978). This equation can then be used to determine the actual diet quality of an area where faecal samples were taken. Because such a regression between diet quality and faecal %N and %P has not been established for Bontebok, the results of the faecal analysis could only be used as relative indications of higher and lower diet quality. No deductions about the actual diet quality of Bontebok were made from this data. It was also assumed that the point where a faecal sample was collected represents the diet quality of that area. This would hold true for the

territorial breeding bontebok, but also to some extend for the free-roaming bontebok that move little after eating (personal observation).

Fresh faecal samples were collected for chemical analysis, and the GPS position of where they were found, recorded. These samples were oven-dried at 60 °C, and then milled using a 1mm sieve. Nitrogen and phosphorus were used as indicators of diet quality (Grant et al. 2001). The faecal samples were analysed for nitrogen content using the standard Kjeldahl method (AOAC 1990). The standard AOAC method was used to analyse the samples for their phosphorous content. Only fresh faeces, not sampled within 12 h after rain, are acceptable for this analysis (Grant et al. 2001). This restricted the number of samples, as samples could be found only where significant numbers of animals occurred. We were unable to collect faeces for all vegetation types.

For each faecal sample, the "probability area" in which it was found was recorded. After testing the faecal samples for N and P (indicating diet quality of the areas where they were found), %N and %P were then regressed against the probability values of the models to determine whether the Dempster-Shafer models predicted areas of higher diet quality.

Slope and visibility (vegetation height) were combined to model predation "risk". Although there is no true predation risk in the BNP (no large carnivores), previous studies (e.g. Van Zyl 1978) have shown that Bontebok tend to be very cautious, especially when drinking water. They are known to prefer open, flat areas (Pienaar 1974) and therefore this model hypothesized that they prefer areas where they can easily see predators from afar, and have few obstacles when escaping.

The above-mentioned same factors were combined as positive effects for displaying territorial rams (i.e. the probability of higher than average densities on flats and areas with high visibility). This was done because, following Dempster-Shafer theory, a low probability of avoidance does not necessarily mean a high probability of preference. David (1973) described the Bontebok social structure as consisting of breeding, territorial males with harems of females as well as a loose bachelor herd of

nonbreeding males (and a few nonbreeding females). Only the territorial breeding herds contribute to population growth and, thus, long-term densities of the Bontebok. We hypothesized that breeding rams would prefer territories with high visibility for females and allowing increased mobility for defending the territory. If these social factors were the reason for the observed preference of the flats, it would be expected that this model would be a better predictor of the distribution of territorial males than for the other Bontebok.

Van Zyl (1978) has shown that, in summer, Bontebok would normally drink water about once a day, whereas they do not need permanent water points in the rainy season. Distance to water was thus combined with the diet probability map to give combined food-and-water probabilities. Finally, a combined model was mapped to include all the factors, because it is possible that all these factors might play some role in Bontebok habitat selection.

Statistical analysis was done in Statistica 6.1 and Microsoft Excel 2000, using the Resampling Stats Excel Add-in version 2.0 for Windows (Simon 1995). The predictive models were tested using best-fit linear regression. ANCOVA was used to compare the regressions between different groups (e.g. to determine if the "social model" was a better predictor for territorial Bontebok than for other animals). Because visibility in the predator-avoidance model and the social model were dependent on vegetation whereas the water-and-habitat model directly included the vegetation model, a high level of correlation between factors would be expected, making these Dempster-Shafer models unsuitable for a multiple regression approach.

RESULTS

For the habitat type-fire model the results were marginally non-significance for %N ($p=0.058$), but were not significant for either %N or %P ($p>0.05$). For the habitat type-vegetation index model, a weak ($r^2=0.20$ for %N and $r^2=0.19$ for %P), but significant ($p<0.05$) positive relationship between probability of Bontebok preference and faecal quality were found. This confirmed that the habitat type-vegetation index model (shown in Figure 1) could predict areas of preference by Bontebok if diet is the main factor driving preference. The non-significance of the habitat type-fire model might also indicate that at least some of the probability values given to the different

vegetation types were wrong and that grassiness and vegetation height might not be the only suitable criteria for assigning probability values.

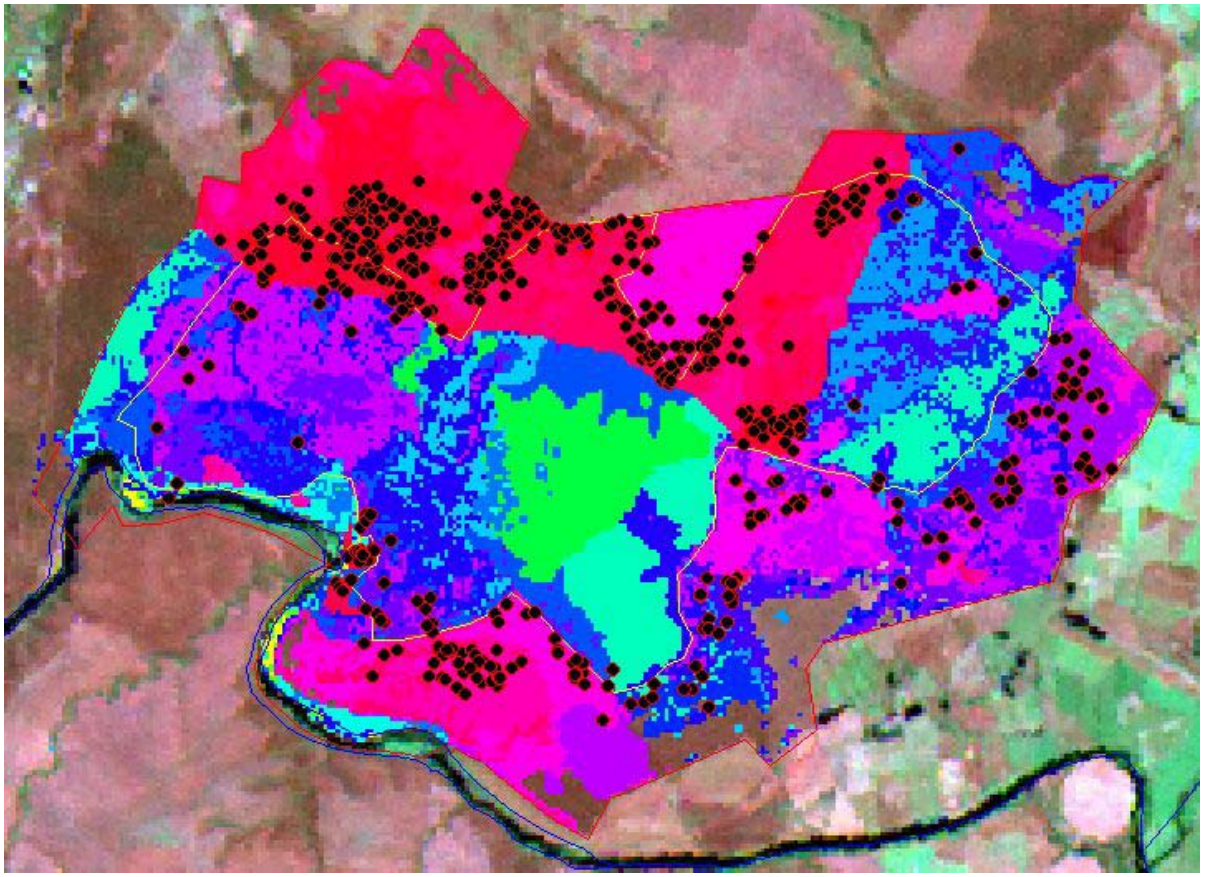

Figure 1 Probability model (habitat type-vegetation index = probability of preference by Bontebok if dietary constraint was the primary determining factor for habitat selection), showing areas with higher probability of preference by Bontebok in red with lower probabilities in blue, still lower probabilities in green, and yellow areas having the lowest probabilities. The small black circles are actual observations of Bontebok herds (not used to construct the model, but shown for comparison).

The power of this model was tested using regression against observed Bontebok densities, giving an indication of the importance of dietary factors in the habitat selection process of Bontebok. This was repeated, using those Bontebok herds where grazing was observed and for the non-territorial herds for whom an ideal free distribution (*sensu* Fretwell & Lucas 1970) was more likely. For the territorial herds, an ideal dominance distribution (Fretwell & Lucas 1970) would be the more appropriate assumption.

Even though the combination of habitat type and fire (habitat type-fire model) did not show a significant correlation to faecal %N or %P, the strength of this model as a general predictor of Bontebok densities were also tested and found to be significant ($p<0.001$, $r^2 = 0.46$) The habitat type-vegetation index model gave a better indication of diet quality according to the faecal analysis, but it did not explain Bontebok distribution any better than the habitat type-fire model. When considering grazing and non-territorial animals only, the habitat type-vegetation index model still showed a significant positive correlation ($p<0.001$), with $r^2=0.32$ for observations of grazing and $r^2=0.33$ for non-territorial animals.

The alternative hypothesis that predator avoidance strategies played the most important role in Bontebok density distribution, was tested by using the Dempster-Shafer model as described in the methods above. It produced the map shown in Figure 2. The predator risk avoidance model did not have a significant effect on the density distribution of Bontebok ($p>0.05$). However, if only resting animals are considered, a significant ($p<0.01$), but weak ($r = -0.15$) negative correlation between "predation risk" and bontebok densities could be shown. Overall, this model did not explain the Bontebok density distribution as well as the diet quality model.

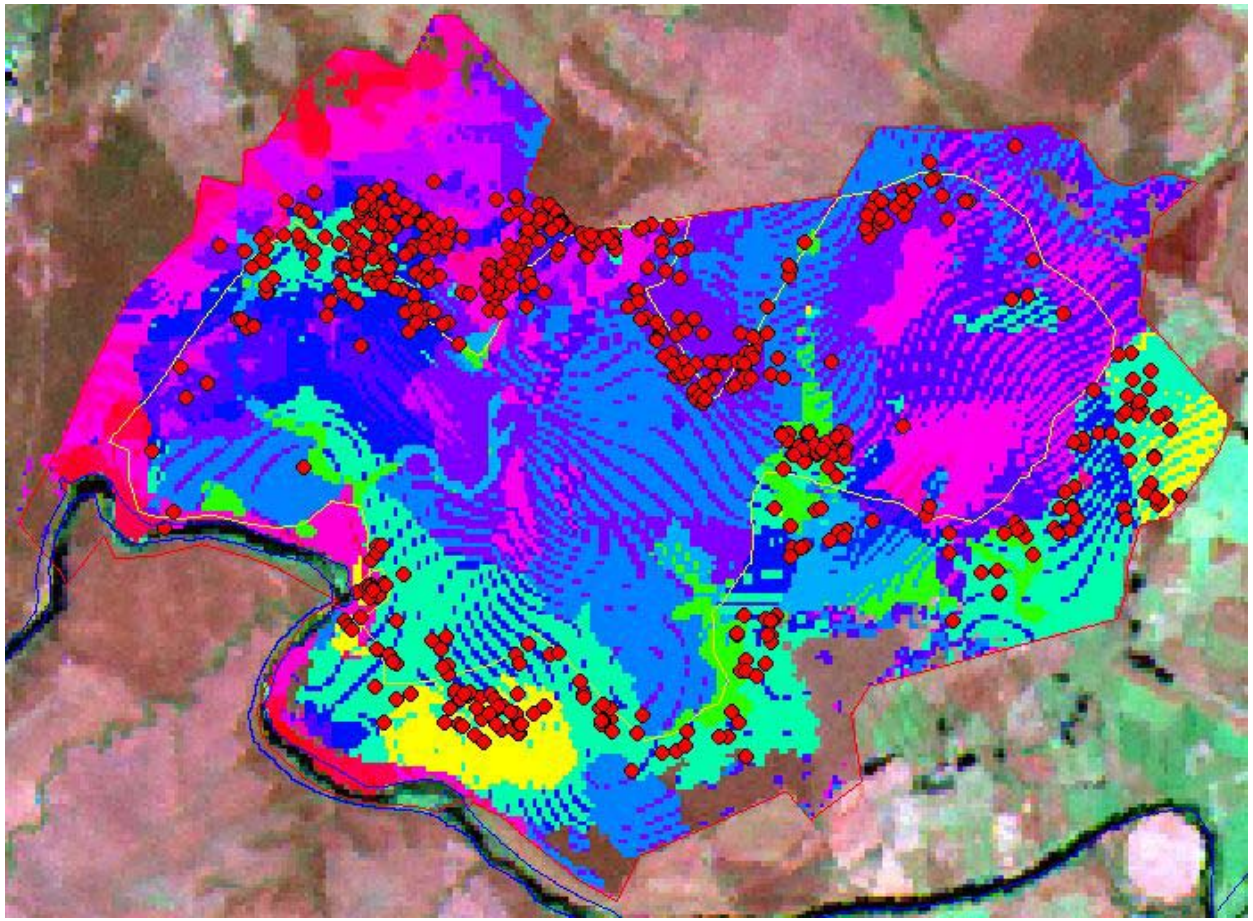

Figure 2 Assuming that Bontebok prefer flat, open areas in order to escape predators, this map shows areas that had a higher probability of being avoided by Bontebok in red, blue areas are intermediate and green to yellow indicate areas with a low probability of being avoided by Bontebok because of "predation risk".

Thereafter, we combined the preference probability map of the distance from water with the habitat type-vegetation index model. Regression showed it to give a significant prediction of Bontebok densities ($p<0.001$) with a slightly better power of explanation ($r^2=0.40$) than the model with habitat type, fire and vegetation index only.

To test if social interactions, specifically preference for habitats where displaying to females and rival males are more visible, determines Bontebok density distribution, it was necessary to not only show a significant preference for those areas, but to demonstrate that territorial males differed from other animals with regard to this preference. The assumption was that if only territorial males showed a preference for these habitats, while others had a negative or indifferent reaction to the predicted areas, it would provide evidence that social factors determine this density pattern. After log-transformation, the data for the social model were still not normally distributed. For this reason, bootstrapping was used to test if the regression slopes for territorial males and nonbreeding animals differed significantly. There was a significant difference ($p<0.05$) between the preference of the predicted "prime territories" for territorial and non-territorial animals. The densities of non-territorial animals showed a non-significant correlation with the predicted probability of preference, while territorial animals showed a slightly positive ($r=0.12$), but significant ($p<0.05$) preference for the areas predicted by the model.

The last alternative hypothesis to be considered was that all of the above-mentioned factors together played a role in the habitat preference of Bontebok. The resulting map produced by this model is shown in Figure 3. When the predicted probability of Bontebok preference was regressed against the observed densities, a significant correlation ($p<0.001$) was found. The explanatory power of this model ($r^2= 0.49$) was better than that of any single other model. Moreover, when that part of the population that is most likely to approach an ideal free distribution, viz. the non-territorial Bontebok, are considered on their own, there is a noticeable increase in explanatory power ($p<0.001$, $r^2= 0.61$). This agrees with the idea that they are more likely to respond to habitat changes in an ideal and free manner (*sensu* Fretwell & Lucas 1970) than territorial animals.

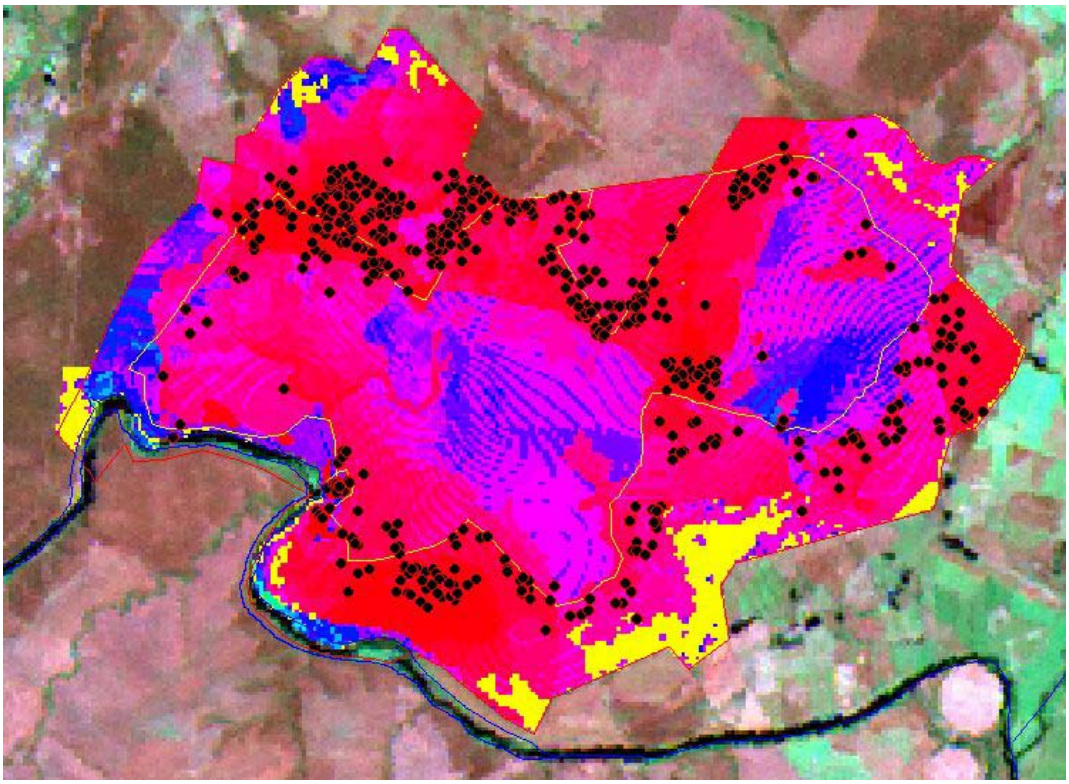

Figure 3 The combined map of Bontebok preference probability. The strength of this model can be seen by the fact the most of the actual Bontebok observations (the black dots) were inside the red areas indicating high probability of preference according to the model. The yellow indicate areas of no knowledge, given a subjective probability of 0.5 for preference by Bontebok. The blue and greenish areas indicate areas with a lower probability of *preference* by Bontebok, but not necessarily with a high probability of being avoided. This is thus only a partial model in that it doesn't indicate the areas unsuitable for Bontebok.

DISCUSSION

Sustainable stocking rates

Hobbs & Hanley (1990) showed that habitat densities can be used to determine "carrying capacity" if three conditions are met: 1) The population is ideal and free, 2) environmental conditions lead to long-term stable equilibrium between animals populations and limiting resources, and 3) an equilibrium was already established when the data were obtained. We know that the assumption of ideal free distribution above doesn't hold for our study (Fretwell & Lucas 1970). The concept of equilibrium in nature has also been under severe criticism (Ellis & Swift 1988, De Leeuw & Tothill 1993, McLeod 1997, Peel et al. 1999). It is ninetheless interesting to see how much the observed densities of our data differ from the ecological carrying capacity as estimated from historical data. Using historical data, the "ecological carrying capacity" for Bontebok in the Bontebok National Park was estimated to be a population size of 220, or a density of about 0.079 animals/ha (Luyt & Ward: submitted). We observed a mean density of 0.067 bontebok/ha along the transect (Luyt & Ward: submitted). If we extrapolate the densities in each habitat type by using the total area of each in the Park, we get an even lower 0.058 bontebok/ha. This is because the Park includes some habitats that were not seen in our transect (and thus were considered as having an animal density of zero), but also because there was probably a systematic undercount of the real number of animals in the transect area. Even in relatively low vegetation, bontebok that were lying down might be missed, causing an undercount bias (cf. Krebs 1989). Thus, these results show that the data are not really suitable for estimating absolute values of bontebok population size.

Almost all definitions of "carrying capacity" assume one of two management aims (Caughley 1976): either the maximization of production (and possible off-take) (= economic carrying capacity) or the maximum population size (= ecological carrying capacity). Both of these aims might be inappropriate for a nature reserve where the management aim is to maximize biodiversity. No explicit reference to this concept of a "biodiversity carrying capacity" could be found in the literature and little is available to indicate what stocking rates would benefit biodiversity most. Even a simple identification of biodiversity with species richness might be inappropriate, because high species richness may be found in areas of high disturbance (e.g. Begon

et al. 1996, Proulx & Mazunder 1998), which is presumably not what we want in a conserved area (De Leo & Levin 1997). This issue was also not addressed adequately in the present study and is worthy of more future research.

Habitat preferences and the factors behind it

A preferred habitat was defined implicitly as a habitat area with significantly higher than average densities of animals. Bontebok density distribution was seen to be correlated to years since last fire (younger veld preferred), vegetation type (grassy habitats preferred) and in the dry season, distance to water (habitats closer to drinking water preferred) (Luyt & Ward: submitted). Both temporal and spatial scale (Baily et al. 1996) as well as social structure (Van Horne 1983), played a role. Some habitat factors, such as permanent water points, change little over time. Water availability had similar effects on all social groups, but differed seasonally in importance. Fire was one factor for which free-ranging Bontebok showed a great preference and it was expected to also increase the quality of the permanent territories where it occurred. The higher density of kids in recently burned areas (Luyt & Ward: submitted) appears to confirm this.

In sum, territorial densities should be expected to give better long-term indications of habitat quality than overall bontebok density distribution alone. Bontebok show preference for certain vegetation types, but there are slight differences between the preferences of free-moving and territorial animals. The fact that present territorial densities do not necessarily reflect present habitat quality was confirmed by the differences between territorial densities and the density distribution of kids (personal observation). Breeding females are known to stay at least part of a year with the same territorial male, but also to simply abandon a territory (sometimes only temporarily) or to change to the territory of another male (David 1973 and personal observation). Their densities might give an indication of habitat preferences at intermediate time scales. All of this would indicate that it makes sense to consider either short-term or long-term habitat preferences. The spatial scales used in this study could not quantify the importance of smaller grazing lawns or individual plant species in the habitat preferences of Bontebok. However, Novellie (1987) has shown that Bontebok show relatively little selection between plant species, the grass height being more important.

Although lower level selection usually manifests on higher spatial levels as well (Baily et al. 1996), it should be kept in mind that some lower-level spatial selection criteria might have been missed in the present study. This could be important if the results are used to identify areas of Bontebok habitat preference outside the BNP.

When considering the factors driving habitat preferences, one can consider different scales, ranging from the level of "bite" to the level of "home range" (Bailey et al. 1996). At each of these levels, different factors act as selection criteria, ranging from nutrient concentration and plant size up to topography, water availability, competition and forage abundance. The factors that we considered as potential explanations for the observed density distributions were mostly at the larger spatial scales for which using a GIS is most suitable. To avoid the pitfall of simply using present densities to infer habitat quality (Van Horne 1983), a number of different alternative hypotheses were modelled as GIS Dempster-Shafer models. They were built by each assuming a different factor or combination of factors as the determining factor that will best explain Bontebok habitat preference. Deciding on the factors to include and test, was done mostly by examining the literature. The assumption was made that the model giving the best prediction of bontebok densities, would be the one most likely to have identified the real determining factor responsible for the habitat preferences of Bontebok. It was found that a combined model had the best predictive power for bontebok densities and that, of the individual factors considered, diet quality was probably the most important. However, the final model had an r^2 value of only 0.49, which suggests that other factors may be involved. One possible way to do this, would be to include probabilities of avoidance for all the factors for which only the probabilities of preference have been used. As mentioned previously, the Dempster-Shafer model makes a clear distinction between low probability of preference and high probability of avoidance (Shafer 1976). This is actually a strength of this approach not adequately used in the present study, which focused on preference rather than avoidance.

We consider the use of Dempster-Shafer GIS modelling as a very useful and underutilized tool in habitat studies where much uncertainty exists. Although we tested our predictive Dempster-Shafer models with data to determine which models

best predicted bontebok densities, it is possible to use the same kind of models as tools of adaptive management (Grossman et al. 1999) in situations where the factors driving habitat preferences of the species have already been identified. It can also be useful for identifying areas with higher and lower probabilities of being preferred habitats for the re-introduction of a species whose driving factors of habitat selection are known. We consider this a better solution than the simple absence/presence GIS models used in the past (e.g. Fabricius & Coetzee 1992, Mace et al. 1999).

Aknowledgments

We wish to thank the personnel at Bontebok National Park for all their assistance and Swellendam Backpackers for providing sleeping facilities and space for data capture. Our thanks also to BEM labs for doing most of the chemical faecal analysis. This material is based upon work supported by the National Research Foundation of South Africa under Grant number 2053674 to David Ward.

References

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1990. Official Methods of Analysis of the Association of Official Analytical Chemists. AOAC, Arlington.

BAILEY, D.W., GROSS, J.E., LACA, E.A., RITTENHOUSE, L.R., COUGHENOUR, M.B., SWIFT D.M. & SIMS, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386-400.

BEGON, M., HARPER, J.L., & TOWNSEND, C.R. 1996. Ecology: individuals, populations and communities. 3rd Ed. Blackwell Science, Oxford.

BEUKES, P.C. 1984. Some aspects of the ecology of the Grey Rhebok (*Pelea Capreolus*, Forster 1790) in the Bontebok National Park. MSc Thesis, University of Stellenbosch, Stellenbosch. [In Afrikaans with English abstract]

BODENSTEIN, V., MEISSNER, H.H. & VAN HOVEN, W. 2000. Food selection by Burchell's zebra and blue wildebeest in the Timbavati area of the Northern Province Lowveld. *South African Journal of Wildlife Research* 30: 63-72.

CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. *Applied Biology* 1: 183-246.

DAVID, J.H.M. 1973. The behaviour of the bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift fur Tierpsychologie* 33: 38-107.

DE LEEUW, P.N. & TOTHILL, J.C. 1993. The concept of rangeland carrying capacity in sub-Saharan Africa - myth or reality. In: Behnke, R.H. Jr., Scoones. I. & Kerven, C. (Eds), Range ecology at disequilibrium (pp. 77-88). Overseas Development Instituite, London.

ELLIS, J.E. & SWIFT, D.M. 1988. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. *Journal of Range Management* 41: 450-459

ERASMUS, T., PENZHORN, B.L. & FAIRALL, N. 1978. Chemical composition of faeces as an index of veld quality. *South African Journal of Wildlife Research* 8: 19-24.

FABRICIUS, C. & COETZEE, K. 1992. Geographic information systems and artificial intelligence for predicting the presence or absence of mountain reedbuck. *South African Journal of Wildlife Research* 22: 49-55.

FRETWELL, S.D. & LUCAS, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

GRANT, C.C., MEISSNER, H.H. & SCHULTHEISS, W.A. 1995. The nutritive value of veld as indicated by faecal phosphorous and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. *Koedoe* 38: 17-31.

GRANT, C.C., PEEL, M.J.S., ZAMBATIS, N. & VAN RYSSEN, J.B.J. 2001. Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range & Forage Science* 17: 81-92.

GROSSMAN, D., P. L. HOLDEN & COLLINSON R. F. H 1999. Veld management on the game ranch. In: Tainton, N. M. (ed), Veld management in South Africa, (pp. 261-279). University of Natal Press, Pietermaritzburg.

GRUNOW, J. O. 1980. Food and habitat preferences among some large herbivores on African veld. *Proceedings of the Grassland Society of Southern Africa* 15: 141-146.

HOBBS, N.T. & HANLEY, T.A. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54: 515-522.

HOBBS, N.T. & SWIFT, D.M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49: 814-822.

KREBS, C. J. 1989. Ecological methodology. Harper Collins, New York.

MACE, R.D., WALKER, J.S., MANLEY, T.L., AKE, K. & WITTINGER, W.T. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* 13: 367-377.

MACLEOD, S.B., KERLEY, G.I.H. & GAYLARD, A. 1996. Habitat and diet of bushbuck *Tragelaphus scriptus* in the Woody Cape Nature Reserve: observations from faecal analysis. *South African Journal of Wildlife Research* 26: 19-25.

MCLEOD, S.R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542.

MCNAUGHTON, S. J. 1999. What is good science? *Natural Resources & Environment* 13: 513-518.

MUYA, S.M. & OGUGE, N.O. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. *African Journal of Ecology* 38: 62-71.

NOVELLIE, P. 1987. Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe* 30: 1-17.

O'CONNOR, T.G. 1992. Patterns of plant selection by grazing cattle in two savanna grasslands: A plant's eye view. *Journal of the Grassland Society of Southern Africa* 9: 97-104.

PEEL, M.J.S., BIGGS, H. & ZACHARIAS, P.J.K. 1999. The evolving use of stocking rate indices currently based on animal number and type in semi-arid heterogeneous landscapes and complex land-use systems. *African Journal of Range & Forage Science* 15: 117-127.

PIENAAR, U. DE V. 1974. Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 17: 185-195.

PROULX, M. & MAZUNDER, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581-2592.

ROOKMAAKER, L.C. 1991. The scientific name of the Bontebok. *Zeitschrift für Säugertiekunde* 56: 190-191.

ROWE-ROWE, D.T. 1982. Influence of fire on antelope distribution and abundance in the Natal Drakensberg. *South African Journal of Wildlife Research* 12: 122-129.

SHAFER, G. 1976. A mathematical theory of evidence. Princeton University Press, Princeton.

SIMON, J.L. 1995. Resampling stats: User's guide. Resampling Stats Inc., Roseville.

TAINTON, N. M. 1999. Production characteristics of the main grazing lands of South Africa. In: Tainton, N.M. (Ed.), Veld Management in South Africa (pp. 46-52). University of Natal Press, Pietermaritzburg.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

VAN ZYL, L. J. 1978. The water requirements and drinking habits of Bontebok *Damaliscus dorcas dorcas* (Pallas, 1766) in the Bontebok National Park. MSc thesis. University of Stellenbosch, Stellenbosch. [In Afrikaans with English abstract]

WATSON, L.H. & OWEN-SMITH, N. 2000. Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology* 38: 130-137.

WILSON, D.E. & REEDER D.M. (Eds). 1993. Mammal species of the World. Smithsonian Institute Press, Washington DC.

WRENCH, J.M., MEISSNER, H.H. & GRANT, C.C. 1997. Assessing diet quality of African ungulates from faecal analyses: the effect of forage quality, intake and herbivore species. *Koedoe* 40: 125-136.

YAGER, R.R., FEDRIZZI, M. & KACPRZYK, J. (Eds). 1994. Advances in the Dempster-Shafer theory of evidence. John Wiley & Sons, New York.

Chapter 4
Conclusions

Sustainable stocking rates

Using historical data, a rough indication of the "ecological carrying capacity" was found for Bontebok in the Bontebok National Park. The method is essentially the same as that used by Sharkey (1970) and East (1984) among others, who included the effects of rainfall and soil nutrient status in their calculations. It amounts to counting the biomass or numbers of animals occurring naturally in an area over a long time period, and using the average value as the carrying capacity. The value of this method can be queried on a number of points, but it can still be useful as a baseline study to check that short-term studies/models are realistic. One important factor to consider is that the studies of East (1984) and that of Sharkey (1970) in respect to East Africa concern a fairly natural ecosystem with both migration and active predators playing a role in the numbers of herbivores. According to Jarman & Sinclair (1979), higher densities of migratory species can occur in an area compared to resident species; this may be even higher than K according to Auger & Bravo de la Parra (2000). Fryxell et al. (1988) give a possible explanation for this phenomenon by suggesting that the numbers of migratory species are probably determined by the environment (bottom-up control) whereas resident species are more vulnerable to control by predators (top-down control). It is also important to note that these studies did not only include long temporal scales, but also large spatial scales. This method might be applicable at these scales only (as is argued by Peel et al. 1999) and not for a restricted population such as Bontebok in the BNP.

Assuming that relatively constant environmental factors caused the original increase and subsequent stabilisation in population growth, a population size of about 275 Bontebok was found to be more-or-less the maximum sustainable. This translates into a maximum stocking density of about 0.098 animals per ha. However, this stocking density would not include the possible long-term negative effect that the animals might have on the vegetation. The rainfall in the driest year was about 80% of the mean rainfall. To be safe, an average stocking density of about 80% of this

"ecological carrying capacity" might therefore be better (cf. Saltz et al. 2004). This gives a population size of 220 or a density of about 0.079 animals/ha, which is slightly less than the present population of about 230 animals. It should be kept in mind that this is an average value only, and numbers in the park have fluctuated a lot since 1973 (De Graaff et al. 1976), with a low of about 190 in 1988 and a peak of about 380 in 1981. These stocking rates are probably sustainable because there has been relatively little change in the vegetation since the study by Grobler & Marais in 1967. This stocking density of 12.73 ha/animal (0.079 animals/ha) is a lot higher than the one of 22 ha/animal estimated by Boshoff et al. (2001). It was also shown that above-average recruitment could be expected in a year that follows a year of high rainfall. Stocking rates need to be adapted to the situation in specific years and an adaptive management strategy (Grossman et al. 1999) is therefore advocated.

Almost all definitions of "carrying capacity" assume one of two management aims (Caughley 1976): either the maximization of production (and possible off-take) (= economic carrying capacity) or the maximum population size (= ecological carrying capacity). Both of these aims might be inappropriate for a nature reserve where the management aim is to maximize biodiversity. No explicit reference to this concept of a "biodiversity carrying capacity" could be found in the literature and little is available to indicate what stocking rates would benefit biodiversity most. Even a simple identification of biodiversity with species richness might be inappropriate, because high species richness may be found in areas of high disturbance (e.g. Begon et al. 1996, Proulx & Mazunder 1998), which is presumably not what we want in a conserved area (De Leo & Levin 1997). This matter is a shortcoming of this research project as well and worthy of more research in future.

Habitat Preferences and the factors driving it

Van Horne (1983) has shown examples of a number of situations where densities of animals do not reflect habitat quality preferences. Three environmental and three species characteristics that might cause this were:

1. If there are seasonal periods of high stress, but observations are made in the season with abundant food and with less extreme weather, wrong conclusions about

habitat quality may be drawn. This was avoided in the present study by sampling in all seasons.

2. If there are large temporal variations in habitat quality, present density might be more representative of past habitat quality than of the present situation. This is the case with fire in the BNP. If we are interested in ascertaining present habitat preferences, the free-ranging bachelor bontebok would give the best indication because they adapt to habitat changes on a daily basis. For indications of longer-term quality, territorial bontebok should give a better indication, because they need to live with their habitat choice for a longer time period. However, the possibility does exist that the present distribution of territorial males might be the result of singular past events. We concur with David (1973) that the long period spent by male bontebok in free-ranging bachelor herds before establishing their own territories (they are sexually mature at age 3, and territorial only after age 5-6), allows them sufficient time to assess the relative long-term quality of most available habitats.

3. Patchiness may cause a decoupling of animal densities and actual habitat quality because movement between adjacent source and sink habitats can result in greater transient densities in sink habitats than would be expected from the latter's habitat quality. In most cases, this should not create a problem because we would expect higher long-term densities in the source habitat if it is indeed higher in quality. A problem connected to the extreme patchiness of the vegetation in Bontebok National Park (T. Kraaij personal communication) is the existence of small, high quality patches within a general habitat of relatively low quality. It is not always apparent how important these patches are in determining habitat choice and the percentage contribution of these patches to habitat quality.

4. Patchiness can be misleading if there are strong social dominance factors in the population (i.e. the distribution of animals is not ideal and free *sensu* Fretwell and Lucas 1970). In this case, dominant animals would settle in the higher quality habitats and prevent sub-dominants from settling there, leading instead to a source-sink situation with higher densities of subdominants in sink habitats than the densities (of dominants) in source habitats. Fortunately, this is unlikely to occur in the present study because personal observations have confirmed the general findings of David (1973) that the bachelor herd simply overruns the territory of any territorial male bontebok. This happens both because these bachelor rams do not compete for females and also because their numbers are so great that the territorial male would spend more

energy to chase them away than what he can gain from simply grazing together (i.e. the cost of defence > benefits of exclusion). David (1973) found that the territorial male and his harem of females would occasionally move to unoccupied areas of his territory in these situations.

5. High reproductive capacity was another confounding factor identified by Van Horne (1983). If a population has this characteristic as well as the dominance structure mentioned above, this could lead to very high densities in sink habitats following good conditions, because of high reproduction in the source habitats.

6. Generalist species may occur in densities that do not reflect true habitat quality. This would be significant when they are used as indicator species for a number of different species, which is not the case in the present study.

Hobbs & Hanley (1990) continued where Van Horne left off. Whereas Van Horne specifically considered populations that are not ideal or free (*sensu* Fretwell & Lucas 1970), Hobbs & Hanley showed that even for ideal free populations, density might not reflect habitat quality. They considered situations where the limiting factors (Liebig 1840, quoted in Boughey 1968) are not substitutable. In other words, both quantity and quality of a resource contribute to habitat quality. As mentioned before, this can lead to situations where high resource quality habitats are chosen when the population is at low density, but high resource quantity habitats preferred at high densities. This effect will only occur when high resource quality habitats are also low in resource quantity and low resource quality habitats are high in quantity. Their conclusion is that habitat densities can only be used to determine “carrying capacity” (Hobbs & Hanley 1990) if three conditions are met: 1) The population is ideal and free, 2) environmental conditions lead to long-term stable equilibrium between animals populations and limiting resources, and 3) an equilibrium was already established when the data were obtained. They defined carrying capacity as "the capability of land to maintain and produce animals of a given species", which agrees well with the definition of habitat quality of Van Horne (1983). We know that the assumption of ideal free distribution above doesn’t hold for our study. The whole concept of equilibrium being reached in nature has also been under severe criticism (Ellis & Swift 1988, De Leeuw & Tothill 1993, McLeod 1997, Peel et al. 1999). However, it is still interesting to see how much the observed densities of our data differ from the ecological carrying capacity as estimated from historical data. We

observed a mean density of 0.067 bontebok/ha along the transect, compared to the estimated carrying capacity of 0.07857 bontebok/ha. If we extrapolate the densities in each habitat type by using the total area of each in the Park, we get an even lower value of 0.058 bontebok/ha. This is because the Park includes some habitats that were not seen in our transect (and thus were considered as having an animal density of zero), but also because there was probably a systematic undercount of the real number of animals in the transect area. Even in relatively low vegetation, bontebok that were lying down might be missed, causing an undercount bias (cf. Krebs 1989). The data are thus not really suitable for estimating absolute values of bontebok, as is also shown by these results.

There was a seasonal change in the density distribution of Bontebok with regards to distance from permanent water points. Significantly higher densities were found closer than 200 m to water in the dry season whereas intermediate distances were preferred in the wet season. For the other species, no significant effect was shown. This is probably because they either roamed over greater distances in a day than Bontebok, and therefore could reach permanent water from everywhere in the Park, or because the sample sizes were simply too small to pick up any effects that existed.

The factors driving habitat preferences can be considered at different scales, ranging from the level of "bite" to the level of "home range" (Bailey et al. 1996). At each of these levels, different factors act as selection criteria, ranging from nutrient concentration and plant size to topography, water availability, competition and forage abundance. The factors that we considered as potential explanations for the observed density distributions were mostly at the larger spatial scales for which using a Geographic Information System (GIS) is most suitable. To avoid the pitfall of simply using present densities to infer habitat quality, a number of different alternative hypotheses were modelled as GIS Dempster-Shafer models. They were built by assuming a different factor or combination of factors as the determining factor that will best explain Bontebok habitat preference. Deciding on the factors to include and test was done mostly by examining the literature. The assumption was made that the model giving the best prediction of Bontebok densities would be the one most likely to have identified the real determining factor responsible for the density distribution

of Bontebok. It was found that a combined model had the best predictive power for Bontebok densities and that, of the individual factors considered, diet quality was probably the most important. However, the final model had an r^2 value of 0.49, which indicates that there is much unexplained variance. One possible way to further our understanding, without using more data, would be to include probabilities of avoidance for all the factors for which only the probabilities of preference have been used. As mentioned before, the Dempster-Shafer model makes a clear distinction between low probability of preference and high probability of avoidance (Shafer 1976). This is actually a strength of this approach not adequately used in this study, which focused more on preference than avoidance.

Management implications

Single species conservation aimed at one species, the Bontebok *Damaliscus pygargus pygargus*, led to the concomitant conservation of the largest patch of conserved coastal Renosterveld (Rebelo 1996). Recently, the main objective of the Bontebok National Park has changed to conserving overall biodiversity, rather than simply one species. Partly for this reason, more land was acquired and several questions arise about what changes this should entail in the management of the BNP. What would be the contribution of this study to answering some of these questions? Factors that were considered here and might be applicable include vegetation types, fire, water points, Bontebok habitat preference, diet quality, sustainable stocking rates, interactions with other species and the social structure of the Bontebok population.

Although a detailed vegetation study was not the main consideration in this project, a general comparison with the data of Grobler & Marais (1967) showed little evidence of any large changes in the plant communities over the intervening period (1967-2004). Subject to the results of further research, the management practices up to the present do not seem to require great changes with the new emphasis on biodiversity instead of Bontebok conservation. In general, a diverse and highly heterogeneous vegetation was found. Vegetation in the Bontebok National Park could be classed into three main groups, viz. the Fynbos areas on the higher levels, the Renosterveld areas on the richer alluvial soils and the riverine and *Acacia karroo* tree communities. It is not known how much the vegetation on the newly acquired land differs from these

vegetation types, but it includes some shale-derived soils, which are more typical of Renosterveld than the alluvium on which it occurs in the present Bontebok National Park (Rebelo 1996). This could imply that different management practices will be needed in these areas.

This study has focused mostly on the requirements and density distributions of the Bontebok. However, any grazing system is actually a system of dynamic interaction (Caughley 1976). This implies that it is not just the plant community that influences the Bontebok densities as shown in this study, but that Bontebok can also be expected to have some influence on the vegetation. Heady (1975) made a distinction between stocking as a daily phenomenon, forage use as a seasonal phenomenon and grazing at a longer time scale. He defines overstocking as something that can be corrected in a day; overuse (overutilization) can be corrected in one growing season, while the effects of overgrazing may take several years to reverse. We could add the term "degradation" to include both the direct effect on vegetation and the effects on physical resources that may not be reversible in human time scales (cf. Dean et al. 1995). The fact that the effect of animals on their habitat is not always taken into account by carrying capacity models (Van Gils et al. 2004) is one of the major criticisms that can be raised against this concept. In general, it can be hypothesized that grazing and fire have opposite effects in the vegetation community of BNP, with fire tending to make it more grassy and grazing tending to result in more shrubby vegetation. However, because of the possibility of positive feedback loops and the creation of grazing lawns, a simple relationship like this might not be true for Bontebok.

One important aspect where at least some caution is needed, is in regards to fire management. Since 1975 (Beukes 1984), a burning program has been followed in the park. Areas that were considered as higher in "floristic quality" or that had a low potential for grass production, were protected from fire as much as possible. The remaining areas had different burning cycles of between 3 and 8 years, with the grassier areas burnt more frequently. In practice, because of accidental wildfires, a more pragmatic approach was followed. This appears to have promoted heterogeneity in the BNP with mean periods between fires ranging from 3.7 years up to more than 29 years. However, in 2001, only about 65 ha was burnt. The whole bachelor herd

concentrated on that area for about a year and effectively created one huge grazing lawn from an area that previously had both shrubs and grasses. Three years later (2004), the effects are still visible (Figure 1). This would imply that the burning of only a single small patch in a specific year might have long-term negative effects on the vegetation. Here, the short-term habitat preference of Bontebok led to effects that were consistent with the negative impacts of heavy grazing, even though the overall numbers of Bontebok were relatively low (181 – 217). On the other hand, the study by Beukes (1984) does not mention any negative effects on the vegetation caused by the high Bontebok population (425) in 1981. While we are clearly open to the criticism of arguing from a lack of evidence, we still feel that this can be considered as illustrating the fact that habitat preferences can be more important in management of a natural system than simply using the concept of a fixed "carrying capacity". Because of the preference of Bontebok for recently burnt veld, it is one of the main recommendations of this study to have longer time periods between fire events and to burn larger areas rather than too small an area. Alternatively, it might be feasible to burn a number of widely-spread smaller patches simultaneously. We also believe that, in general, even for grassy Renosterveld areas, three year burning cycles are too frequent. In general, the adaptive management that was used in the past to take account of wildfires worked fairly well. However, there were some areas that our study identified as *Leucadendron* Fynbos (e.g. R16 & R 17) that were on similar four year burning cycles as were used for the Renosterveld areas (Beukes 1984). Although they showed true fire frequencies of 3.8 and 6.5 years, these are probably still too short for this vegetation type.

Figure 1 The effects of fire followed by heavy grazing. These 2 areas are adjacent to each other and should presumably be similar in terms of plant species. The area on the left burnt in 1999, but already shows a diversity of species and growth-forms. The area on the right burnt in 2001, followed by very heavy grazing by Bontebok and has not recovered two years later.

Overall, water points are adequate at present, but this might not be true for the new areas added to the BNP. The use of water availability to manipulate the Bontebok densities has not been investigated properly. Even if practical, this will only work in summer as this study has confirmed that Bontebok are independent of permanent water in winter, but may need to drink regularly in summer.

One of the original considerations for the re-introduction of Mountain Zebra and Red Hartebeest to the Bontebok National Park (Novellie 1987) was that they might have a facilitating role by grazing down the taller grasses to heights more acceptable to Bontebok and thus lessen the dependence on fire. Unfortunately, the numbers of both of these species have remained too low to have any real influence on the vegetation. In addition, there has been an alarmingly large drop in Grey Rhebok population size from 200 – 210 animals in 1980 to the present levels of about 35. Browsers such as Grey Rhebok might inhibit the increase of shrubs in areas where they browse, leading

to an increase in grasses because of reduced competition, and possibly more food for Bontebok and the other grazers. One obvious way to increase the number of species (as a measure of biodiversity) is to introduce more species to an area. However, this should be done carefully so as not to increase competition with the herbivore species already in the BNP. It is possible that the BNP functions as a founder-controlled community in terms of herbivores (Begon et al. 1996) with the Bontebok preventing successful establishment of competing herbivore species. Here it should also be kept in mind that the population size of Bontebok in the BNP is still well below the minimum viable population size given by Lande (1988) as 500 (cf. Gilpin 1996). Even if an effective population size of 500 might be enough to prevent negative genetic effects in the lobg term, Lande (1988) showed that demographic effects could still cause extinctions (Begon et al. 1996). We would therefore not recommend a reduction of the Bontebok population below 200 to facilitate the introduction of other species. It is important that there be enough breeding males for ensuring the persistence of the Bontebok population. Because new territorial males come from the pool of bachelors, it might also be important for the bachelor herd not to become too small.

In terms of direct competition between the herbivore species, this study suggests that except for Grey Rhebok, the other species generally do not have the same habitat preferences as Bontebok. Grey Rhebok, being a browser, has only about 5% dietary overlap with Bontebok (Beukes 1984) and although they prefer the same habitats, they are unlikely to compete. It is also possible for the two larger species to have a grazing pattern more like that of Buffalo in the Hluhluwe Game Reserve (Perrin & Brereton-Stiles 1999), which were seen to revisit the same widespread patches repeatedly in a rotational manner. Random monthly transects such as was used in this study might miss this pattern. If this pattern is the case for these species, the grazing system of Bontebok National Park could have similarities to that in Hluhluwe, with both Bontebok and White Rhino being relatively unselective short-grass grazers and Red Hartebeest and Mountain Zebra resembling Buffalo as tall-grass grazers with greater grass species selectivity. The big difference would be that in the BNP, the short-grass grazers contribute most to the overall biomass while the opposite is true in Hluhluwe.

Because this study was done at a single site, caution is advisable in using the results when considering the re-introduction of Bontebok to other areas. For example, examining the density distribution of Bontebok in the present Bontebok National Park will not prevent problems such as the copper deficiency experienced by Bontebok in the original BNP. In general, diet quality factors were shown to be the most important in determining habitat preferences of Bontebok. General guidelines are that a suitable habitat for Bontebok should include sufficient grass. Although it might not be the preferred species, because of the fact that *Cynodon dactylon* is fond of higher nutrient soils (Van Oudtshoorn 1999), this species might be used as an indicator that Bontebok will use a certain habitat. However, this study has also shown that Bontebok will use any of the habitat types available, provided that it burnt recently. In that case, the area considered for the introduction should be large enough that reasonably large patches of it can be burnt at least every second year, without any specific patch being burnt more often than applicable for its vegetation type (4-8 years for Renosterveld and grassy areas, 13-20 years for Fynbos). Water should be available in summer. Although topography was less important than diet factors, it can still be observed that Bontebok generally prefers open, flat areas.

Further research

Grazing lawns

It was found that the territorial male Bontebok preferred those vegetation types that had small patches of either grazing lawns or naturally occurring *Cynodon dactylon* lawns regardless of the surrounding vegetation. Moreover, there are indications that the territorial "dung sites" (David 1973) of these males were responsible for initiating at least some of the grazing lawns (cf. Figure 2). This hypothesis is still untested in the BNP, but it is likely that a positive feedback loop (e.g. Person et al. 2003) starts with local enrichment of the soil caused by the dung middens of the territorial male Bontebok. The trampling effect would also decrease shrub cover in the site. An increase in grass species and annuals that prefer soils high in nitrogen and that are usually higher in nutritional content themselves, would likely increase grazing. This will result in grazing tolerant, but productive grass species such as *Cynodon dactylon* becoming dominant. The higher nutritional value of these species would lead to increased Bontebok densities in that patch and might result in a true grazing lawn,

larger in extent than the original dung site. Increased Bontebok densities would lead to further enrichment of the soil from faeces and urine, causing a local positive feedback loop. It was interesting that, in some vegetation types (e.g. *Leucadendron-Stipagrostis* fynbos), no grazing lawns were observed in spite of the presence of territorial males. More research on this is needed. Another question arising from this is "Does the presence of grazing lawns in a certain area decrease or increase the grazing pressure on the surrounding vegetation?" (cf. McNaughton 1984).

Figure 2 It is hypothesized that the dung sites of territorial Bontebok males are the starting point of a positive feedback loop leading to the creation of high-production *Cynodon dactylon* grazing lawns.

There has been considerable controversy over the statement that grazing might increase plant production (e.g. Belsky 1986). Maschinski & Whitham (1989) showed that there exists a continuum of reactions to grazing by plants and even that the same grass species might react differently in different seasons and under different conditions. For the species they tested, they found a lower probability of compensation for herbivory when there was competition with other plants, at lower nutrient levels and also when herbivory occurs later in the growing season (see also

Proulx & Mazunder 1998). This last-mentioned factor was found to be important in the Bontebok National Park by Novellie (1987) who recorded that the grass species that were most heavily grazed (>50% of leaves removed) by Bontebok shortly after fire (*Pentaschistis eriostoma, Merxmuellera stricta, Themeda triandra, Eragrostis curvula* and *Stipagrostis zeyheri*), were avoided later on and showed up to a sevenfold increase in canopy spread cover. At the time of Novellie's study, there were no Mountain Zebra or Red Hartebeest in the BNP. He correctly predicted that recently burnt grass would be mostly too short for utilization by these species, but would be acceptable by them 20 months later (Novellie 1987). The fire preference shown by these species in the present study confirms this prediction.

Dempster-Shafer modeling in GIS

Most habitat studies done using a Geographic Information System, make use of simple presence-absence data (e.g. Fabricius & Coetzee 1992, Mace et al. 1999), classifying habitats only as suitable or unsuitable for a certain species. The approach followed in this study seems to be an improvement by producing a model showing probabilities of preference. This is probably closer to the real situation where habitat preferences are more likely to be a continuum ranging from being totally avoided to being absolutely preferred.

One drawback of the Dempster-Shafer models used here was that there was no weighting attached to the different factors, all of them being considered equally important. Seeing that one of the objectives of this study was to determine the relative importance of these factors, this is not surprising. However, it might be possible to improve the final combined model by including the results of the individual factor models and giving them different weights before combining them. Overall, this study confirms that spatially-explicit Dempster-Shafer models can be a very useful tool to use in habitat predictive models.

Vegetation

It was impossible to test any predictions with regards to particular grass species as factors influencing Bontebok preference, with the possible exception of *Cynodon dactylon* that was known to be totally dominant in the grassy lawns of Habitat 1. This can be identified as a priority in future research. In particular, it would be very useful

to examine the effects of fire because it is possible that fire has more of an effect on the vegetation than grazing. The fynbos areas that we considered as too frequently burnt (R17 & R16) are both adjacent to protected fynbos areas with similar plant species and appear to actually be the same communities. This gives the ideal opportunity to find out to what extent fire diminishes the biodiversity of fynbos. The fire of January 2003 swept through a large part of the BNP, including most of the fynbos areas. Because these areas differ in fire frequency, but experienced their most recent fire at the same time, studies should be able to examine the effects of fire frequency rather than simply the effect of time since last fire.

Faecal analysis

Faecal analysis can be used both to determine the grass species (it is not very effective for shrubs) (MacLeod et al. 1996) as well as the chemical quality of herbivore diets (Erasmus et al. 1978). The fact that faecal samples were not found in all vegetation types made this method much less useful in this study than it could potentially be. Future studies that are less concerned with the behavioural aspects of Bontebok (and can thus afford more disturbance of the animals) should be able to collect more faecal samples and make better use of the results from faecal analysis, especially with regard to the plant species being eaten, and the amount of overlap (and potential competition) between the different herbivore species.

Acknowledgements

Thanks to the following persons and organizations: South African National Parks for all their help and for the privilege of working in Bontebok National Park, BEM Labs for the chemical analysis, Prof. Daan Nel for help with the statistics, Swellendam Backpackers for providing accommodation during field trips, Benjamin Walton for helping with plant identification and to my supervisor Prof. D.Ward, for lots of patience and help. To my Creator, both for creating nature and giving me the opportunity to study it, the greatest thanks of all. This material is based upon work supported by the National Research Foundation of South Africa under Grant number 2053674 to David Ward.

References

AUGER, P. & BRAVO DE LA PARRA, R. 2000. Methods of aggregation of variables in population dynamics. *Life Sciences* 323: 665-674.

BAILEY, D.W., GROSS, J.E., LACA, E.A., RITTENHOUSE, L.R., COUGHENOUR, M.B., SWIFT D.M. & SIMS, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386-400.

BEGON, M., HARPER, J.L., & TOWNSEND, C.R. 1996. Ecology: individuals, populations and communities. 3rd Ed. Blackwell Science, Oxford.

BELSKY, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* 127: 870-892.

BEUKES, P. C. 1984. Some aspects of the ecology of the Grey Rhebok (Pelea Capreolus, Forster 1790) in the Bontebok National Park. MSc Thesis, University of Stellenbosch, Stellenbosch. [In Afrikaans with English summary]

BOSHOFF, A.F.,. KERLEY, G.I.H & COWLING, R.M. 2001. A pragmatic approach to estimating the distributions and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions* 7: 29-43.

BOUGHEY, A.S. 1968. Ecology of Populations. Macmillan Company, New York.

CAUGHLEY, G. 1976. Wildlife Management and the Dynamics of Ungulate Populations. *Applied Biology* 1: 183-246.

DAVID, J.H.M. 1973. The behaviour of the Bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift fur Tierpsychology* 33: 38-107.

DEAN, W.R.J., M.T. HOFFMAN, M.E. MEADOWS & MILTON S.J. 1995. Desertification in the semi-arid Karoo, South Africa: review and reassessment. *Journal of Arid Environments* 30: 247-264.

DE GRAAFF, G., VAN DER WALT P.T. & VAN ZYL, L.J. 1976. Population composition of the Bontebok *Damaliscus dorcas dorcas* in the Bontebok National Park during January 1974 *Koedoe* 19: 67-74. [In Afrikaans with English summary].

DE LEEUW, P.N. & TOTHILL, J.C. 1993. The concept of rangeland carrying capacity in sub-Saharan Africa - myth or reality. In: Behnke, R.H. Jr.,

Scoones. I. & Kerven, C. (Eds), Range ecology at disequilibrium (pp. 77-88). Overseas Development Instituite, London.

DE LEO, G.A. & LEVIN, S. 1997. The multifaceted aspects of ecosystem integrity. *Conservation Ecology* 1: 3.

EAST R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* 22: 245-720.

ELLIS, J.E. & SWIFT, D.M. 1988. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. *Journal of Range Management* 41: 450-459

ERASMUS, T., PENZHORN, B.L. & FAIRALL, N. 1978. Chemical composition of faeces as an index of veld quality. *South African Journal of Wildlife Research* 8: 19-24.

FABRICIUS, C. & COETZEE, K. 1992. Geographic information systems and artificial intelligence for predicting the presence or absence of mountain reedbuck. *South African Journal of Wildlife Research* 22: 49-55.

FRETWELL, S.D. & LUCAS, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

FRYXELL, J.M., GREEVER, J. & SINCLAIR, A.R.E. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131: 781-798.

GILPIN, M. 1996. Forty-eight parrots and the origins of population viability analysis. *Conservation Biology* 10: 1491-1493.

GROBLER, P. J. & MARAIS, J. 1967. The vegetation of the Bontebok National Park, Swellendam. *Koedoe* 10: 132-146. [In Afrikaans with English summary]

GROSSMAN, D., P. L. HOLDEN & COLLINSON R. F. H 1999. Veld management on the game ranch. In: Tainton, N. M. (ed), Veld management in South Africa, (pp. 261-279). University of Natal Press, Pietermaritzburg.

HEADY, H.F. 1975. Rangeland management. McGraw-Hill, New York.

HOBBS, N.T. & HANLEY, T.A. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54: 515-522.

JARMAN, P.J. & SINCLAIR, A.R.E. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair, A.R.E. & Norton-Griffiths, M. (Eds), Serengeti: Dynamics of an ecosystem (pp.130-163). University of Chicago Press, Chicago.

KREBS, C. J. 1989. Ecological methodology. Harper Collins, New York.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455-1460.

MACE, R.D., WALKER, J.S., MANLEY, T.L., AKE, K. & WITTINGER, W.T. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* 13: 367-377.

MACLEOD, S.B., KERLEY, G.I.H. & GAYLARD, A. 1996. Habitat and diet of bushbuck *Tragelaphus scriptus* in the Woody Cape Nature Reserve: observations from faecal analysis. *South African Journal of Wildlife Research* 26: 19-25.

MCLEOD, S.R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542.

MCNAUGHTON, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* 124: 863-886.

MASCHINSKI J. & WHITHAM T.G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1–19.

NOVELLIE, P. 1987. Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe* 30: 1-17.

PEEL, M.J.S., BIGGS, H. & ZACHARIAS, P.J.K. 1999. The evolving use of stocking rate indices currently based on animal number and type in semi-arid heterogeneous landscapes and complex land-use systems. *African Journal of Range & Forage Science* 15: 117-127.

PERRIN, M.R. & BRERETON-STILES, R. 1999. Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *South African Journal of Wildlife Research* 29: 72-80.

PERSON, B.T., HERZOG, M.P., RUESS, R.W., SEDINGER, J.S. ANTHONY, R.M. & BABCOCK, C.A. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecologia* 135: 583-592.

PROULX, M. & MAZUNDER, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581-2592.

REBELO, A.G. 1996. South & South-West Coast Renosterveld. In: Low, A.B. & Robelo, A.G. (Eds), Vegetation of South Africa, Lesotho and Swaziland (veg63.htm). Department of Environmental Affairs and Tourism, Pretoria.

SALTZ, D., WARD, D., KAPOFI, I. & KARAMATA, J. 2004. Population estimation and harvesting potential for game in arid Namibia. *South African Journal of Wildlife Research* 34: 153-161.

SHAFER, G. 1976. A mathematical theory of evidence. Princeton University Press, Princeton.

SHARKEY, M. J. 1970. The carrying capacity of natural and improved land in different climatic zones. *Mammalia* 34: 564-572.

VAN GILS, J.A., EDELAAR, P., ESCUDERO, G. & PIERSMA, T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104: 197-204.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

VAN OUDTSHOORN, F. 1999. Guide to grasses of South Africa. Briza, Pretoria.